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PREDATION AS A FACTOR IN MAINTAINING THE PELVIC POLYMORPHISM IN A CENTRAL ALBERTA POPULATION OF *Culaea inconstans* (Kirtland), (PISCES : GASTEROSTEIDAE).

by

© JAMES D. REIST

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Predation as a factor in maintaining the pelvic polymorphism in a central Alberta population of Culaea inconstans (Kirtland), (PISCES: Gasterosteidae).

submitted by James Douglas Reist

in partial fulfilment of the requirements for the degree of Master of Science

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Supervisor

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Date 19 May 1978

ABSTRACT

Laboratory and field work was conducted to assess the importance of fish and invertebrate predation in maintaining a pelvic polymorphism in Culaea inconstans.

Field work in the Redwater River system (Alberta) indicated a slight geographical and seasonal variation of morph frequencies (fluctuation in frequencies of morphs without the pelvis and in intermediate forms). A causative agent was not identified. No ecological separation with respect to gross habitats was found within any site.

Laboratory behaviour and predation experiments using Esox lucius as predators indicated that morphs with the pelvis are at a morphological advantage relative to without morphs. Specifically, the withs escape more often after capture by small pike but this advantage, which is size dependent, disappears if the ratio of predator to prey length exceeds four times. Total body depth of prey and jaw width of predator are the critical morphological parameters. Both morphs exhibit similar defensive behaviour when confronted by a pike; however the withouts had a slight advantage in that they avoided such situations better than withs. The behavioural response to pike predators is influenced by age of prey and probably past experience since considerable individualism in behaviour was evident. Stomach collections of wild pike indicated that this behavioural difference contributes to significant selective predation upon the with morphs in Wakomao Lake.

Laboratory predation by Lethocerus americanus was found to be random on each morph.

Laboratory predation by Aeschna sp. nymphs was heavy upon without morphs in the single experiment conducted.

Laboratory predation and behavioural experiments with Dytiscus sp. larvae showed heavy predation upon with morphs due to their closer approaches to the predator.

This evidence is used to support the hypothesis of a predation maintained polymorphism in which the pelvic morphs - with and without - are at a relative advantage at certain times during certain predatory regimes. Thus the frequency of with and without morphs observed at any point in time, is a balance between previously exerted predatory forces. Additional predators present in the field but not investigated, and additional uses of the pelvic spines probably also influence the polymorphism frequencies.

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INTRODUCTION

Ford (1945) defines polymorphism as the simultaneous occurrence of two or more distinct forms of a species in the same population. A further differentiation is made between a transient polymorphism that occurs when one form replaces another (such as melanism in Biston betularia) and a balanced polymorphism in which the distinct forms are maintained at equilibrium frequencies in the population (Ford, 1975). The latter case includes numerous situations involving Batesian mimicry as well as the well-documented examples of the gastropod, Cepaea nemoralis (Ford, 1975). The term morph is used in the present context to mean the observed phenotypic classes of such populations.

Gasterosteid fishes are well known for their morphologically variable populations and the brook stickleback, Culaea inconstans (Kirtland) is no exception. A cline in pelvic and dorsal spine lengths has been demonstrated (Nelson, 1969) and numerous populations of Culaea in mid-central Alberta and Saskatchewan have a high proportion of individuals totally lacking the pelvic skeleton (Nelson, 1969, 1977; Nelson and Atton, 1971; Nelson and Paetz, 1974). Other authors have noted that throughout its range Culaea also exhibits a cline in dorsal spine number usually with a strong mode at five, a smaller one at six, with a range of four to seven (Lawler, 1958; Nelson, 1969; Scott and Crossman, 1973).

The pelvic polymorphism is not restricted to Culaea but is observed in three of the five gasterosteid genera. Gasterosteus aculeatus shows loss of the pelvic apparatus in freshwater lakes on the Queen Charlotte Islands (Moodie and Reimchen, 1976a,b); Texada Island, B.C. (Larson, 1976); and California (Bell, 1976); as well as Pliocene fossil material from Nevada (Bell, 1974). Pungitius pungitius populations from Alberta and Ireland also show pelvic polymorphism (Nelson, 1971; Nelson and Paetz, 1972). Variation in other morphological structures (e.g. lateral scutes, gill rakers) is also known in Gasterosteus from both Palearctic and Nearctic waters (Hagen and Gilbertson, 1972, 1973; Wootton, 1976).

Four possible pelvic states are observed in polymorphic Culaea populations: complete presence (with morph), complete absence (without morph), spined intermediate (intermediate, spined morph) and unspined intermediate (intermediate, spineless morph). Illustrations and morphological descriptions may be found in Nelson (1969, 1977) and Nelson and Atton (1971). This polymorphism has at least a partial genetic basis (Nelson, 1977) hence is of interest for its evolutionary implications.

Pelvic development in Culaea occurs relatively late in ontogeny and is extended over a period of time (Nelson and Atton, 1971). Geographic variation in the time of appearance and formation of the complete skeleton has also been noted, with eastern populations showing earlier development (e.g. Crooked Lake, Indiana Culaea have a complete pelvis at 14 mm) than western populations (e.g. Astotin Lake fish with pelvis complete at 21-24 mm), (Nelson and Atton, 1971). Relative growth in the length of the pelvic and dorsal spines varies with age. The increase in spine length in smaller fish (< 30 mm) is positively allometric but above this size it becomes negatively allometric (J. S. Nelson, pers. comm.; personal observation), although considerable site specific variation of these generalities does exist. The implications of differences in growth rate or timing of the appearance of the pelvic spines have not been investigated.

Predation has been implicated in maintaining many of the polymorphisms noted above. The effectiveness of the dorsal and pelvic spines as anti-predator devices, at least in choice situations involving Gasterosteus, has been shown by Hoogland et al. (1957). A correlation between the low ratio of forage fish to predators and the short-spined (and polymorphic) northwestern part of Culaea's range was noted by Nelson (1969). This lack of choice of prey items for the predators may have created local selection pressures which favoured escape responses such as streamlining or lightening the body (Nelson, 1969, p. 2444). Subsequent work has lent some support to this hypothesis; populations with a high percentage of without morphs tend to be found in landlocked lakes (Nelson and Atton, 1971) which are deficient in piscivorous fishes (Nelson and Paetz, 1974). The lack of experimental testing of this hypothesis prompted the present study.

The study was designed in four sections, to ascertain the role of predation in maintaining the polymorphism:

1. Field work on a polymorphic population established morph frequency, distribution and gross ecology, stability of the polymorphism and yearly variation in morph frequency.

2. Laboratory predation experiments investigated the

possibility of selective predation upon the morphs by northern pike (*Esox lucius*), (Pisces: Esocidae); *Lethocerus americanus* (Insecta: Hemiptera); *Dytiscus* sp. (Insecta: Coleoptera); and *Aeschna* sp. (Insecta: Odonata) predators.

3. Laboratory behaviour experiments were designed to detect and elucidate any behavioural differences in the morphs relevant to predation (especially by pike).

4. Stomach collections of pike from the 'natural' population permitted the interpretation of laboratory findings with reference to the field situation.

In an approach such as this, certain assumptions must be made which have little supporting evidence at the present time. Factors other than predation are assumed to have little or no effect on the experimental results. The contribution of mutation or developmental anomalies to the morph frequency is considered to be negligible.

THE STUDY AREA AND STUDY POPULATION

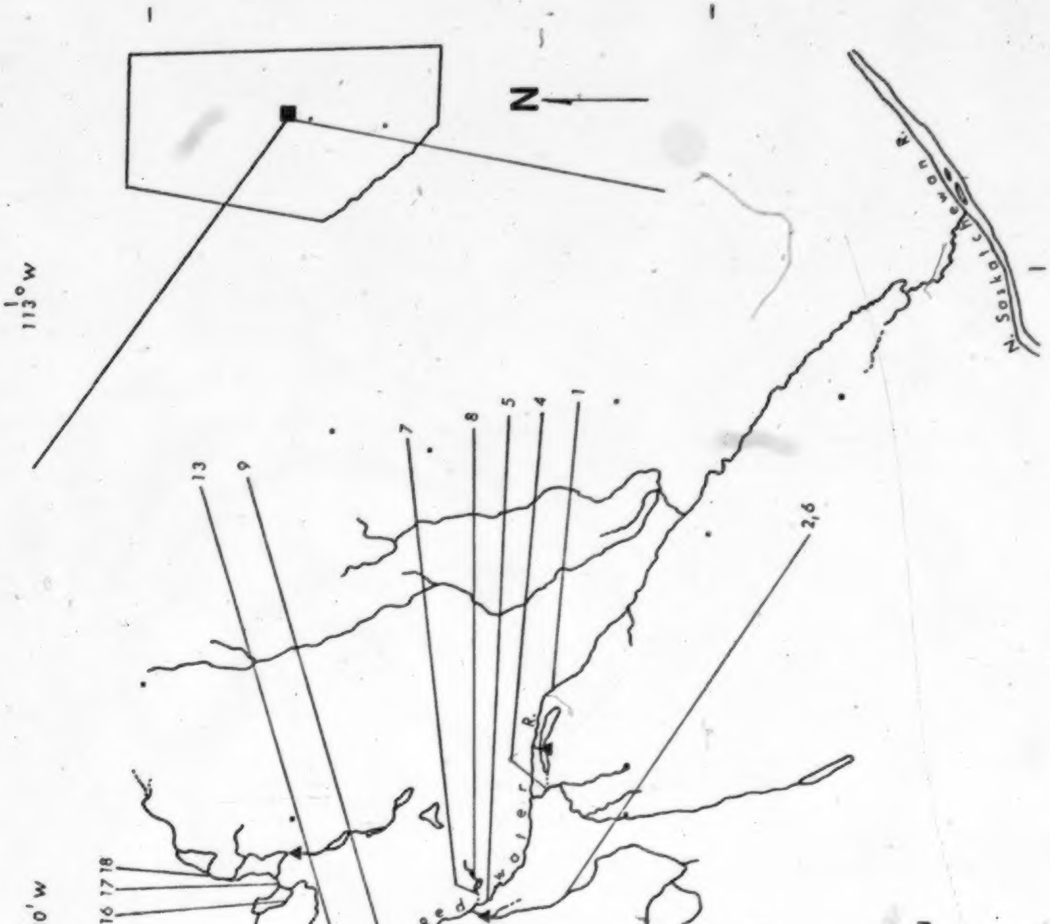
Introduction

The Redwater River system (Figure 1) lies about 80 kilometers (km) north of Edmonton and is a tributary to the North Saskatchewan drainage. The specific study site, Wakomao Lake, 54°09' N 113°32' W, was chosen since it has a large polymorphic population of Culaea which experience predation by both invertebrates and northern pike.

Wakomao Lake (Appendix 1, Figure 7) is a small (about 325 hectares), eutrophic lake lying in flat marshy country (Government of Alberta Hydrographic Survey, 1960). It is the most proximate of a series of shallow lakes draining into the Redwater system. Maximum depth is about 2.5 meters (m) at the southern end with the average depth being between 1 and 1.5 m (present study and Government of Alberta Hydrographic Survey, 1960). Most of the shoreline is marshy with extensive emergent macrophyte beds (Appendix 3, Table 31) but the southeast margin (windward with respect to the prevailing winds) is sand beach. Extensive shallow marshes at the north and south ends and the west side of the lake are inundated at various high water periods.

Water inflow to the lake is by two small creeks at the north end, outflow is by a meandering moderate sized creek to the Redwater River at the south end. Extensive beaver activity on these creeks (as well as most of the Redwater system itself) restricts fish movements between the various lakes, the Redwater River and the

Figure 1: Redwater River system. Numbers refer to collection sites from Table 1. ▲ = areas sampled but no Culaea found, ■ = towns. The major study area was Wakomao Lake (#10).


113°W
113°30'W
54°15'N
54°N
N
N. Saskatchewan R.
Red Water R.
Wakomao Lake
Clyde
Vimy
Legal
5 Km
1
2,6
4
5
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7
9
13
12
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North Saskatchewan River. Wakomao Lake is connected to Halfway Lake by a weir controlled canal dug in recent years by the resident. Fish movement into the canal is quite evident especially at high water.

The land surrounding Wakomao Lake is mostly pasture, used lightly by cattle, with several hay fields. Willow (Salix sp.) occurs along the southern margins and the north end of the lake. Extensive areas of the east and southeast shorelines are aspen poplar (Populus tremuloides) and jackpine (Pinus banksiana). Most islands in the lake are also wooded. The lake is subject to light recreational pressures by the residents and some angling for pike occurs in the vicinity of the bridge at the south end.

Wakomao Lake has been the subject of an abortive management program with 25,000 adult yellow perch (Perca flavescens), (Government of Alberta Hydrographic Survey, 1960) stocked in July, 1955. Subsequent efforts at management have been abandoned due to the shallow nature of the lake.

Four species of fish were found in Wakomao Lake in the present study: Culaea inconstans (brook stickleback), Pimephales promelas (fathead minnow), Catostomus commersoni (white sucker) and Esox lucius (northern pike). All are believed to be 'natural' emigrants from the Redwater and ultimately the North Saskatchewan systems.

Methods

The 1976 collections were restricted to the southeast section of Wakomao Lake, Redwater River and Fairydell Creek. In

1977 collections were made from the majority of the water bodies in the system. All collections were made in water depths of 1.5 m or less usually by one of three methods: dipnet, bagseine (8.6 m x 1.35 m deep, 5 x 3 mm mesh size) or electroshocker (Smith-Root, Inc. Type VII). The method chosen depended upon the water body topography, the dipnet being favoured in stream and heavily vegetated areas. Additionally, minnow trap collections were conducted in Wakomao Lake. Each location was sampled so as to avoid collection biases (see Appendix 2) and the fish were immediately preserved in 10% formalin.

Pelvic morphs of preserved sticklebacks are easily scoreable using a sharp probe (Nelson, 1977 describes the categories). All fish under 20 millimeters (mm) standard length were examined for pelvic state under a low power dissecting microscope. Dorsal spine counts were easily made and included all exposed erectile elements. Standard length (SL) was the shortest distance between the tip of the snout and the end of the hypural plate, read on calibrated dial calipers to the nearest 0.1 mm. Some misassignment of pelvic morphs may occur in very small fish since pelvic development occurs from about 13-21 mm SL (Nelson and Atton, 1971). For this reason, fish less than 15 mm SL were considered unassignable to pelvic morph and left out of statistical considerations.

On the basis of vegetation type, time of year and position in the lake, eight habitats are discernible in Wakomao Lake (Appendix 3, Table 31). Dipnet collections from each of these were used to establish any preference by the pelvic morphs.

Statistical comparisons were by normal, row by column chi-square with minimal significance level of $p = 0.05$. Since the two intermediate classes of pelvic morphs were present in low frequencies all chi-square calculations were done with these combined.

Results

Pelvic morph frequency in the Redwater system (Table 1) is relatively constant with some notable exceptions. Sites 6, 8, 13, 15 and 16 contribute heavily to the significant ($p = 0.025$) deviation from typical morph frequencies in the area (e.g. Wakomao Lake). These sites all differ from the normal Redwater situation in environmental parameters which were not quantified in the present study. Fairydell Creek collections (6) for both 1976 and 1977 show an over-abundance of intermediates. It is a sparsely vegetated, slow flowing, spring fed creek with cold water (5-8^{0}C at mid-summer). The beaver pond (8) collection has an over-representation of withs and relatively few withouts. It is a sparsely vegetated, cold water pond which overflows into a bog at the edge of the unnamed lake. The Halfway Lake (13) collection has a paucity of withs and intermediates and an excess of withouts. This collection was from a peaty bog on the west margin of the lake. Halfway Lake differs from the other areas investigated in that it lies in a black spruce (_Picea_ _mariana_) bog basin and seems to have very hard water as evidenced by extensive growths of _Chara_ sp. Halfway Lake is also subject to water draw-down from a cement plant 2 km south. Wakomao Creek (15) in this region is in an area of lowland black spruce-willow bog.

Table 1: Morph frequency in the Redwater River system. Map numbers refer to locations on Figure 1. Most samples are composites from Appendix 1, Tables 28-30. Samples with less than 50 individuals are not included. Intermediate groups combined for chi-square statistics. ‡ indicates samples with anomalous morph frequencies.

		Pelvic Morph Frequency (%)				
		With	Intermediate		Without	
Map #	Site Name		Spined	Spineless		N
1976						
1	Redwater River	73(72.3)	1(1.0)	2(2.0)	25(24.7)	101
2	Fairydell Creek	152(71.0)	5(2.3)	6(2.8)	51(23.8)	214
3	Wakomao Lake	495(68.2)	39(5.4)	31(4.3)	161(22.2)	726
			$X^2 = 8.51$ ($p \cong 0.08$)			
1977						
4	Outflow from Halfmoon Lake	93(70.5)	4(3.0)	4(3.0)	31(23.5)	132
5	Redwater River	402(69.8)	16(2.8)	18(3.1)	140(24.3)	576
6	Fairydell Creek‡	72(68.6)	4(3.8)	6(5.5)	23(21.9)	105
7	Overflow from unnamed lake	51(79.7)	1(1.6)	1(1.6)	11(17.2)	64
8	Beaver Pond‡ Creek	617(76.5)	13(1.6)	21(2.6)	155(19.2)	806
9	Creek south of Wakomao Lake	190(70.1)	9(3.3)	8(2.9)	64(23.6)	271
10	Wakomao Lake	1526(70.6)	73(3.4)	31(1.4)	531(24.6)	2161
11	Slough south of Wakomao Lake	89(70.1)	4(3.1)	1(0.8)	33(26.0)	127
12	Halfway Creek	105(72.4)	4(2.7)	3(2.1)	33(22.7)	145
13	Halfway Lake‡	71(63.4)	1(0.9)	1(0.9)	39(34.8)	112
14	Wakomao Creek	322(70.9)	9(2.0)	10(2.1)	106(23.7)	447
15	Wakomao Creek‡	247(73.3)	1(0.3)	6(1.8)	83(24.6)	337
16	West Bridges‡ Lake	205(71.2)	4(1.4)	4(1.4)	75(26.0)	288
17	Bridges Creek	205(72.4)	9(3.2)	7(2.5)	62(21.9)	283
18	Duggans Creek	226(74.1)	11(3.6)	7(2.3)	61(20.0)	305
			$X^2 = 44.47$ ($p = 0.025$)			

This collection had too few intermediates. West Bridges Lake (16) with too few intermediates, is atypical in that it is a relatively deep, cold water lake not as eutrophic as Wakomao Lake. The habitat of the remaining sites resembled Wakomao Lake closely - heavily vegetated, slow flowing or standing water and moderately to very eutrophic.

There is no association between pelvic morph and dorsal spine frequencies (Table 2); thus the analysis of the dorsal spine variation was restricted (see predation experiments and stomach collections).

The earliest year (1971) for which substantial collections of Culaea have been made from Wakomao Lake shows no difference in pelvic morph frequency from the 1977 frequencies (Table 3). Between 1976 juveniles and the surviving (i.e. overwintering) 1977 adults there is an indication of morph frequency variation with decreased overwinter survival of intermediates and withouts (Table 4). Partial restoration of the original frequencies in the next 1977 sample containing scoreable young-of-the-year suggests the possibility of a periodicity in the frequency changes. However, the 1976 collections may have an overrepresentation of intermediate morphs (cf. 1971 and 1977). Within the 1977 cohort there is a slight but non-significant tendency for an increase in with and intermediate frequencies and a decrease in without frequency, as fish grow older.

Table 5 shows no association of the morphs with any defined habitat in the lake with the notable exception of no occurrence of

Table 2: Pelvic and dorsal morph association in Wakomao Lake (both years combined).

	Frequency of Dorsal Spine Morph (% of morph)			
Pelvic Morph	4	5	6	7
with	21 (2.4)	590 (66.4)	276 (31.1)	1 (0.0)
intermediate	2 (2.3)	61 (71.8)	22 (25.9)	0 (0.0)
without	11 (3.9)	196 (70.0)	73 (26.1)	0 (0.0)
Total	34 (2.7)	847 (67.6)	371 (29.6)	1 (0.1)

$X^2 = 5.24$ ($p \cong 0.5$)

Table 3: Pelvic morph frequency through time in Wakomao Lake.

	Pelvic Morph Frequency (%)				
	With	Intermediate		Without	
Year		Spined	Spineless		N
1971[1]	201 (71.0)	2 (0.7)	11 (3.9)	70 (24.7)	284
1977	1526 (70.6)	73 (3.4)	31 (1.4)	531 (24.6)	2161

$X^2 = 0.03$ ($p \cong 1.0$)

[1] (UAMZ #2989, 2992 taken July 1)

Table 4: Morph frequency change with age of Culaea.

1976 juveniles to 1977 adults.

Year	Frequency of Pelvic Morph (%) with	intermediate	without	N
1976 (76-3,4)	495 (68.6)	70 (9.8)	161 (22.2)	726
1977 (77-2-a)	145 (77.1)	7 (3.7)	36 (19.1)	188
	$X^2 = 8.56$ $(0.01 < p < 0.025)$			
1977 (77-14a-c)	563 (72.5)	43 (5.5)	170 (21.9)	776

Within the 1977 Cohort (Collections: #77-14-a, 77-20-f, 77-24-a and 77-27-a-c taken on 20 vii, 18 viii, 20 ix and 25 x 1977, respectively).

Standard Length (age) group	Frequency of Pelvic Morph (%) with	intermediate	without	N
15-29.9 mm	315 (75.0)	17 (4.1)	88 (20.9)	420
30-39.9 mm	324 (72.5)	31 (6.9)	92 (20.6)	447
40+ mm	106 (77.9)	12 (8.8)	18 (13.2)	136

$X^2 = 9.03$ $(p \cong 0.08)$

Table 5: Morph frequency by habitat within Wakomao Lake (Appendix 3, Table 33 shows individual samples).

Habitat Type	Morph Frequency (%)				N	# of Samples
	with	spined intermediate	spineless intermediate	without		
1 Burred-*Typha* shoreline	111 (65.3)	7 (4.1)	7 (4.1)	45 (26.5)	170	2
2 *Scirpus* shoreline	432 (74.6)	19 (3.3)	9 (1.5)	119 (20.5)	579	4
3 *Myriophyllum*-*Lemna*: washed on shore, floating	325 (69.1)	18 (3.8)	3 (0.6)	124 (26.4)	470	2
4 *Myriophyllum*-rooted on shore submerged	207 (70.2)	8 (2.7)	2 (0.7)	78 (26.4)	295	2
5 Open sand beach less than 5% cover vegetation, *Culaea* here May-June only	236 (68.2)	10 (2.9)	8 (2.3)	92 (26.6)	346	2
6 Submerged algal mats (*Cladophora* sp.- May-June only)	83 (67.5)	6 (4.9)	2 (1.6)	32 (26.0)	123	1
7 Offshore rooted *Myriophyllum*-*Potamogeton*	132 (74.1)	5 (2.8)	0 (0.0)	41 (23.0)	178	2
8 Open, unvegetated water	0 (00.0)	0 (0.0)	0 (0.0)	0 (00.0)	0	2[1]
Total	1526 (70.6)	73 (3.4)	31 (1.4)	531 (24.6)	2161	

$X^2 = 16.67$ ($0.1 < p < 0.5$)

[1] no *Culaea* visually sighted, none taken in surface minnow traps set for 270 trap-hours.

Culaea in open unvegetated water, with exceptions as noted below.

Stickleback Ecology and the Predators of Wakomao Lake

The yearly habitat selection of the Culaea population in Wakomao Lake is varied and seems to be closely tied to the periodicity of cover vegetation and predators. The shallowness of the lake probably results in winter oxygen depletion, but due to restricted waterways the population appears to overwinter there. Adults are sparse and in the limnetic zone after ice break up. Reproduction begins in May and extends to early June, after which the young-of-the-year become numerous in the sparse onshore (sand beach area) vegetation (Carex, Cladophora and some Myriophyllum). Adult fathead minnows are infrequently found in the area. Towards the end of June and beginning of July the young-of-the-year and remaining Culaea adults form large schools (up to 100,000 individuals) in the open water on the sand beaches. An abrupt transition takes place in early August when young fatheads begin schooling in the same area; the Culaea schools break up and the individuals tend to become associated with beds of Myriophyllum and Ceratophyllum which, at about this time, are achieving their peak densities. The sticklebacks remain associated with these vegetation beds until freeze-up.

The predators found in Wakomao Lake (Appendix 3, Figure 8) follow similar seasonal cycles. Northern pike were probably present in moderate numbers at all times but only data for July and August were collected (see stomach section). Pike favour vegetated areas and will enter very shallow water when pursing prey items (pike were taken occasionally in bagseine hauls). Predation by pike on the sticklebacks of Wakomao Lake was likely considerable.

Lethocerus americanus (Belostomatidae: Hemiptera) nymphs and adults were present in low frequencies throughout the summer (Figure 8). They were associated with macrophytes, usually the dense Myriophyllum beds. Their consumption of Wakomao Lake sticklebacks was probably low but constant.

Dytiscus sp. (Dytiscidae: Coleoptera) larvae were very abundant from early June to mid-July (Figure 8), primarily associated with vegetation but at this time the sticklebacks were mostly schooling in the open water. Their predation on the Wakomao Lake population may have been considerable, especially on reproducing adults and newly hatched young which were still in vegetated areas.

Odonate (dragonfly) nymphs were present throughout the year (probably overwinter also) and showed some periods of great abundance (Figure 8). Their predation on the Culaea population was likely considerable.

A superficial survey of the remaining vertebrate and invertebrate fauna yielded a list of other potential predators on the Culaea population (Figure 8). The influence of most of these on the stickleback population, especially the avian piscivores is unknown.

Discussion

Slight correlations of pelvic morph frequency with specific environmental conditions have been noted by Nelson and Atton (1971) - a greater tendency for pelvicless forms to occur in lakes lacking outlets and a larger frequency of anomalous morphs in lakes which have been disturbed. Localities are known in which adjacent but not contiguous lakes have radically different morph frequencies (Nelson, 1977; Nelson and Atton, 1971) and in some there is a tendency for higher without frequencies in lakes lacking piscivorous fishes (Nelson and Paetz, 1974). In the present study most of the morph frequency fluctuation is in the intermediate and without categories in atypical sites in the Redwater system. The various factors which may be correlated with the morph frequency variation are unknown. Nelson (1977) speculates that variation in predation may be the environmental variable causally associated with the polymorphism frequencies. The potential predators and their influences on the populations presumably vary in these atypical situations but the correlation of predator density with morph frequency was not rigorously investigated. The influence of potentially important environmental factors such as variation in calcium and phosphorous ion concentration on pelvic development is unknown.

The lack of association between the dorsal spine count and pelvic polymorphism suggests that these are responding to different causal agents, assuming that the dorsal spine variation has a genetic basis and is not merely a result of the influence of physicochemical parameters on developmental processes.

The short term stability of the pelvic polymorphism has been noted for other lakes, (Nelson and Atton, 1971 and Nelson, 1977), but the frequency in some areas fluctuates from year to year (e.g. Muir Lake collections, J. S. Nelson, pers. comm.). These authors also suggested a tendency for variation in the morph frequency between or within different age classes in Astotin Lake. These findings, the significant change in morph frequency in the 1976 to 1977 samples (fewer intermediates and withouts collected the following spring), and the tendency within the 1977 cohort for fewer withouts being present in samples of older fish might be due to one or more of a variety of causes. Aside from such factors as non-random sampling (see Appendix 2) or differential morph dispersal (unlikely since the same area was sampled and the lake population is believed to be isolated during winter), such change in phenotype frequencies may be due to incorrect assignment to morph, differential reproduction or development, or to differential selection within the generation. Of these latter three factors, the last - differential selection - seems most plausible, since incorrect assessment of phenotype is unlikely at the larger sizes of fish considered and sampling occurred after reproduction and expression of the pelvic condition. The influence of non-random mating upon the morph frequency is unknown and could potentially contribute greatly to observed morph frequencies. The causative selective agent which removes intermediates and withouts is unknown, but by inference from subsequent work, it may be predation. Many more long term observations are necessary to accumulate evidence to support or deny a hypothesis of annual cyclical selection and even to establish the stability of morph frequency.

The lack of morph association with the grossly defined habitats in Wakomao Lake suggests that with respect to the pike predators, and perhaps the invertebrate predators as well, no potential difference in morph availability is evident, at least on an ecological basis. This work does not eliminate the possibility that subtle between morph differences in ecological preferences may exist which would bias morph availability especially to the invertebrate predators. The tendency to shift habitat preferences for at least part of the year may act to minimize some predation on the stickleback population; e.g. by removing them from the site of invertebrate predators.

THE METHODS OF THE PREDATORS

Pike

Northern pike are opportunistic predators (Scott and Crossman, 1973) which prey in a stereotyped manner. Hoogland et al., (1957) and Christiansen (1976) provide detailed descriptions of pike predatory behaviour. This brief summary is based upon their accounts.

The pike orients to its prey after initial detection and then follows one of two possible patterns which depend to some degree upon the prey's behaviour. If the situation is occurring in cover vegetation (or in a confined tank space, present study and Hoogland et al., 1957) or if the prey is unaware, the pike stalks slowly forward until appropriately positioned and then makes a sudden final predatory lunge. If the sequence occurs in an open area where the prey item is more likely to be fleeing, the pike makes a rapid approach, pursuing and snapping at the prey. The former sequence is usually the more successful. At the same time as the jaws are snapped shut the predator sucks water and prey into its mouth. This, combined with the forward momentum of the pike, makes escape unlikely for prey much smaller than the pike. After capture, the prey is manipulated, turned on its side and swallowed, usually head first.

Pike associate with vegetated areas usually in shoreline situations (Diana et al., 1977; Roberts, 1975). Christiansen (1976) has shown that this association is primarily with sparsely to moderately vegetated areas. He suggests that some cover vegetation is necessary for successful predation since it is here that the pike quietly lurks, hidden until a prey item chances to come close. Extremely dense vegetation impedes the predatory act and is avoided by pike (Christiansen, 1976).

Pike rely heavily upon vision and to a lesser extent upon mechanical stimuli for initial orientation to prey items (Christiansen, 1976 and present study). Prey movement or locomotion is important in releasing the final lunge (present study) and pike often turn away from the target fish if such movement is not forthcoming. The pike may be characterized as active foragers early in the year when little vegetation is present (J. Diana, pers. comm.) but become stalking, semi-ambush predators at later times.

Preference for dense cover and less activity in open water, remaining immobile while being stalked and fast or early initiated escape attempts would be distinct advantages to sticklebacks encountering pike predators.

Lethocerus americanus

Lethocerus americanus is a large (up to 6.5 cm long) highly predaceous, aquatic bug capable of taking most large aquatic organisms including tadpoles, frogs and fish (Pennak, 1953). The bug usually sits motionless at or near the surface with its body extending obliguely down (Usinger, 1956), gripping detritus or vegetation. It waits until a prey item blunders between or near the outstretched, raptorial forelegs. Orientation to an approaching prey item is evident. Quick, short snaps of the forelegs may be made at the prey if the bug is especially hungry. The capture response is visually controlled and only when the prey is close enough are the forelegs snapped shut. Immediate insertion of the beak and injection of toxic saliva (Pennak, 1953) dispatches the prey quickly. The liquified contents are then sucked up and the remains discarded. Once caught, escape of the prey is unlikely since the bug quickly clamps all six legs around the item if need be and floats free until the prey is dispatched. Holling (1961) reports that these bugs continue killing prey items even when satiated; hence their influence on a prey population may be considerable, but is dependent upon prey density. _Lethocerus_ may be characterized as a strictly ambush predator.

Culaea does not investigate the bug unless it moves. Individual prey types preferring vegetated areas or approaching closely will be at a disadvantage.

Dytiscus

Dytiscus sp. larvae are large (up to 4.5 cm long) voracious predators which use sickle shaped mandibles for prey capture. The larva anchors itself to vegetation and sits in a typical reverse-C posture with the head capsule and mandibles protruding into the water column. Periodically, the hold is released and the positively buoyant individual floats to the surface for respiratory gas exchange. The larva then swims back to the bottom using legs and body in an undulating fashion. Predation seems to be primarily visual and the larva will make short, up to 2 centimeter (cm) lunges at any prey item which ventures near or near to which it swims. The larvae also swim towards movements made by potential prey. Salivary injections probably cause the prey to quickly succumb, the liquified contents are sucked out, and the remains are discarded. Dytiscids may be characterized as ambush-lunge predators, waiting for the prey to come near, then attempting ~~to~~ capture it by a quick lunge.

Prey fish such as sticklebacks which actively investigate movement of small organisms would easily place themselves in vulnerable positions.

Aeschna

Due to limitations of time and collection problems behaviour of *Aeschna* sp. (Aeschnidae: Odonata) predators was not extensively investigated. The nymphs are primarily bottom feeders but also occur in vegetation at all depths in the water column. In addition, they will also crawl out on projections of detritus and wait for prey items at night (T. E. Reimchen, pers. comm.). If they have the opportunity they will take small sticklebacks at least in the lab, but field work is required to determine if this occurs in the lake for *Aeschna*, as well as the other invertebrate predators.

LABORATORY PREDATION EXPERIMENTS

Methods

Laboratory experiments were conducted to determine the direction and degree of any differential predation on the primary pelvic morphs (with and without). All prey fish were collected from the southeast portion of Wakomao Lake by dipnet or bagseine and transported to flow-through fibreglass holding tanks (59 cm x 48 cm x 120 cm). They were held at ambient (8-17°C) water temperature under natural photoperiod until used. During holding and experiments the prey fish were fed every second day on either live invertebrates from Wakomao Lake (especially *Daphnia* sp.) or commercial frozen brine shrimp (*Artemia* sp.). Mortality was usually low but during a two week period in late July an unknown disease caused many deaths.

Two basic types of experiments were conducted, using either northern pike or invertebrates as predators. All experiments were carried out in natural photoperiod from late summer to mid-winter, the time when sticklebacks tend to be gregarious thus removing biases due to intraspecific agonistic behaviour in the prey fish. However, effects of season upon the relative advantages of the morphs were not controlled and this has been shown to be important in selective predation on *Gasterosteus* (Moodie et al., 1973). Prey fish were removed from the holding tanks and dorsal spine counts made, standard length taken and pelvic state determined prior to the experimental setup. All reasonable attempts were made to exclude individuals of the spineless intermediate group from the without category but as Nelson (1977) notes, the categories spineless (withouts and spineless intermediates) one-spined (intermediate spined) and complete (with) were the best when dealing with live fish. The inclusion of some spineless intermediates in the without category may bias to an unknown degree the results presented. Equal frequencies of with and without morphs (15 of each in pike experiments, 7 of each in invertebrate experiments) were placed in the experimental tanks and allowed to acclimate for six to seven days before the predator(s) was introduced. All experiments were conducted with only one dorsal spine category (either five or six) and the prey were divided into homogenous size groups of small (20-29.9 mm SL), medium (30-39.9 mm SL) and large (40-49.9 mm SL) fish. Cover vegetation when present consisted of Myriophyllum, Ceratophyllum, Potamogeton and filamentous algae from Wakomao Lake.

Pike predators for the experiments were collected as young-of-the-year (8-10 cm SL) from the Redwater River (Figure 1, site 5). Invertebrate predators were collected either at this Redwater site or Wakomao Lake. Predators were held in flow-through tanks and maintained on a variety of live prey - fathead minnows, suckers and sticklebacks of all pelvic types. The pike grew in the course of the experiments but all were between 11 and 18 cm SL. Predator and prey sizes and the ratio for each experimental set is shown in Table 46 (Appendix 4).

A series of experiments conducted in 1976 differed from the above setup in several ways: pike were from the Sturgeon River near

Darwell, Alberta, and were assumed not to have been exposed to polymorphic Culaea either historically (i.e. immediate ancestry) or within their lifetimes since few sticklebacks are found in this river system. No acclimation period was allowed the prey fish. Several sources of prey fish were used; Fairydell Creek (Figure 1, site 2), Wakomao Lake (Figure 1, site 3) and Whitemud Creek (at Highway 39, five km west of Leduc, $53^{0}16^{'}$N $113^{0}38^{'}$W). Prey sizes and dorsal spine categories were mixed. The fish remaining were scored to pelvic morph daily. The pike predators were not changed during the experiment.

Experiments involving pike were conducted in flow-through fibreglass aquaria (52 cm x 32 cm x 76 cm) with a low input flow of ambient water and a single airstone. Pike were changed each morning (1977) and the number of remaining prey determined. When 50% of the prey had been eaten the experiment was terminated and the pelvic morph frequency of the survivors determined. The surviving fish were examined for predator marks caused by contact with pike's teeth. These marks were very characteristic, either rows of conical depressions or elongate slashes on the flanks of the fish. Two types of experimental conditions were investigated - vegetation present and covering 25-50% of surface area of the tank and no cover vegetation present. Thus, there were 12 experimental combinations: 3 size groups X 2 dorsal classes X 2 experimental conditions. Two other series of experiments were conducted. With morphs had their pelvic spines clipped to make them morphologically equivalent to the without morphs. In one series clipped withs and normal withouts were presented in equal frequency for no cover, medium and large prey fish experiments. The second series presented clipped withs in equal frequency to normal withs for no cover, medium and large prey fish experiments.

Three categories of data were forthcoming from the pike predation experiments. The number of each morph consumed is derived by subtracting the number of each morph alive at the termination of the experiment from the starting number. This latter number was adjusted for any mortality of the prey fish due to causes other than predation. Surviving fish marked by the predator are equated with escapes from the predator in subsequent analysis. This measure is obviously biased downward since it is unable to account for multiple escapes, escapes then consumption, or fish not marked during escape. A third basis for comparison is the number of fish attacked by the pike. The number of attacks is the sum of consumed and marked for each morph.

Experiments with invertebrate predators (_Lethocerus americanus_, _Dytiscus_ sp. larvae and _Aeschna_ sp. nymphs) were conducted in standing water plexiglas tanks (29 cm x 29 cm x 37 cm) at room temperature (19^{0}C). A single airstone provided aeration. All tanks had a 1-2 cm layer of sand on the bottom. All experiments were conducted with cover vegetation (25-50% area covered) collected from Wakomao Lake. Small and medium size categories of prey fish were used. Predators were not changed daily. Adult and nymphal _Lethocerus_ were used as single predators; larval _Dytiscus_ and nymphal aeschnids were placed in experiments in threes. Only the number of each morph consumed was analyzed.

Experimental results within each dorsal spine category were tested for heterogeneity (Sokal and Rohlf, 1969), then combined since all experiments within each group were homogeneous. Differences in predation upon five and six spined fish were investigated by subjecting the number of fish eaten from each dorsal spine group compared to the number offered, to normal chi-square. No significant differences were found and results for five and six spined fish were combined unless directional trends were noted, e.g. large five spined fish in cover (pike predator) and Dytiscus experiments.

The data (consumed, marked, attacked) were analyzed using the hypergeometric chi-square method of O'Donald and Pilecki (1970) in the following format:

	Pelvic Morph		
	with	without	total
Number at start	A	B	N
Number eaten	a	b	n

$$\text{where } X^2 = \frac{(aN-An)^2(N-1)}{nAB(N-n)} .$$

Normal chi-square assumes selection occurs from an infinite population of each morph. Since this assumption is not met, the probability of encountering the rarer morph (if selection does occur) diminishes as predation continues. The hypergeometric chi-square test compensates for this.

Results

Pike predation

The 1976 experiments (Table 6) show significant selection for the without morphs from the Redwater River system (Wakomao Lake and Fairydell Creek). No selective predation of either morph occurred in the experiments involving Whitemud Creek fish. No predation marks (escapes) were noted on any fish from the 1976 experiments.

Predation upon unaltered Wakomao Lake morphs (Table 7) by Redwater pike in 1977 is non-selective in most cases. However, for large, five dorsal spined fish in the cover series there is a non-significant trend in each replicate for selection upon the without morph. Comparing corresponding size groups of prey between cover and no cover experiments shows that the X^2 values (a measure of the predation differential between morphs) is always larger in the cover series (ex. small: $0.08 < 0.82$; medium: $0.03 < 0.85$; large $0.22 < 2.58$). Within both the cover and no cover series, as size of prey increases the predation differential becomes greater, especially between medium and large size fish (X^2 from 0.85 to 2.58 and 0.03 to 0.22). Within the cover experiments the non-significant selection is initially against small withouts, reverses to slightly on medium withs and then back to large withouts. Within the no cover series predation is essentially equal on both morphs of each size group.

When presented with morphologically equivalent prey (clipped withs and normal withouts) pike significantly prefer the clipped withs (Table 8) of the medium size group but select neither

Table 6: 1976 pike predation experiments on pelvic morphs (Sturgeon River pike, no cover vegetation, mixed dorsal morphs and mixed size groups).
Note in all tables following: * = $p < 0.05$, ** = $p < 0.025$, *** = $p < 0.01$; Hyper. = hypergeometric; 1 as subscript = Yate's correction for continuity applied.

Source of Prey Fish	Predator/ Prey SL Ratio	With			Without			Hyper. X^2
		Offer	Ate	%	Offer	Ate	%	
Wakomao Lake	3.8	69	23	33	66	36	55	6.12**
Fairydell Ck.	3.3	24	7	29	23	14	61	4.67*
Whitemud Ck.	3.3	47	23	49	49	26	53	0.16

Table 7: Pike predation on unaltered pelvic morphs from Wakomao Lake, 1977 (Redwater River pike; dorsal morphs separated in replicates then combined if no differences were noted).

Conditions	Predator/ Prey SL Ratio	With			Without			Hyper. X^2
		Offer	Ate	%	Offer	Ate	%	
Cover vegetation								
small	5.1	104	44	42	105	51	49	0.82
medium	4.3	85	48	56	85	42	49	0.85
large								
5 dorsal	3.6	43	18	42	43	26	60	2.94
6 dorsal	3.6	44	21	48	41	22	54	0.29
combined		87	39	45	84	48	57	2.58
No cover vegetation								
small	4.2	59	26	44	56	29	52	0.08
medium	4.1	75	37	49	75	36	48	0.03
large	3.6	58	29	50	57	26	46	0.22

prey type from the large size group.

There is non-significant selection of clipped withs over normal withs for the medium size group (Table 9) but no selection for either prey type of the large size category.

The effect of altering the with morphs so they are morphologically equivalent to withouts may be seen by comparing the percent consumption of both morphs (medium size group) between no cover, intact experiments (Table 7) and no cover, clipped with/normal without experiments (Table 8). Withs are consumed 49% and 61% while withouts are consumed 48% and 39%, respectively. That is, morphological equivalence increases predation upon medium sized, with morphs. However, morphological equivalence does not have a similar effect on large withs (50% and 42%).

All escapes of unaltered fish, with one exception, were by large prey (Table 10, X^2 within each morph in each experimental series is very significant). Similar trends are seen in the experiments involving altered morphs (Tables 11 and 12) but medium fish are marked more. In all cases except large, clipped with/normal with experiments, the unspined (without) or despined morphs did not escape as often. A significant difference between morphs is evident if the results are pooled for intact prey (X^2 = 3.84*, Table 10) and clipped withs/normal without prey (X^2 = 7.59***, Table 11). Alteration of (clipping) the morphs reduces but does not eliminate the escapes (cf. Table 10 and 11 X^2 values). Cover vegetation causes a decrease in the differential escaping by the morphs.

Table 8: Pike predation on altered withs and normal without morphs (no cover, dorsal morphs separate then combined).

Size	Predator/ Prey SL Ratio	Clipped Withs			Without			Hyper. X^2
		Offer	Ate	%	Offer	Ate	%	
Medium	3.9	88	54	61	89	35	39	8.55***
Large	3.7	43	18	42	44	23	52	0.93

Table 9: Pike predation on normal and altered with morphs (no cover, dorsal morphs separate then combined).

Size	Predator/ Prey SL Ratio	Normal Withs			Clipped Withs			Hyper. X^2
		Offer	Ate	%	Offer	Ate	%	
Medium	3.9	30	11	37	30	17	57	2.37
Large	3.6	30	15	50	30	14	47	0.07

Table 10: Escapes (predator marks) of unaltered pelvic morphs.

Conditions	With Survivors			Without Survivors			Hyper. X^2
	Unmarked	Marked	%	Unmarked	Marked	%	
Cover vegetation							
small	60	0	0	54	0	0	0.00
medium	37	0	0	43	0	0	0.00
large	40	8	17	33	3	8	1.66
	$X^2 = 13.36_1$**			$X^2 = 6.66_1$*			
No cover vegetation							
small	33	0	0	27	0	0	0.00
medium	37	1	3	39	0	0	1.05
large	20	9	31	26	5	16	3.47
	$X^2 = 14.67_1$***			$X^2 = 8.04_1$*			
All pooled	227	18	7	222	8	3.5	3.84*

Table 11: Escapes (predator marks) of altered withs and normal without morphs.

	Clipped With Survivors			Without Survivors			Hyper.
Size	Unmarked	Marked	%	Unmarked	Marked	%	X^2
Medium	30	4	12	52	2	4	2.49
Large	17	8	32	18	3	14	3.64
	X^2 = 3.64			X^2 = 2.72			
Pooled	47	12	25	70	5	7	7.59***

Table 12: Escapes (predator marks) of normal and altered with morphs.

	Normal With Survivors			Clipped With Survivors			Hyper.
Size	Unmarked	Marked	%	Unmarked	Marked	%	X^2
Medium	16	3	16	12	1	8	0.59
Large	9	6	40	7	9	55	0.70
	X^2 = 2.52			X^2 = 5.56$_1$*			
Pooled	25	9	26	19	10	35	1.19

Table 13: Attacks by pike on unaltered pelvic morphs.

	With			Without			Hyper.
Conditions	Offer	Attack	%	Offer	Attack	%	X^2
Cover vegetation							
small	same as predated (Table 7)						
medium	same as predated (Table 7)						
large	87	47	54	84	51	51	0.78
No cover vegetation							
small	same as predated (Table 7)						
medium	75	38	51	75	36	48	0.11
large	58	38	63	57	31	54	1.47

Table 14: Attacks by pike on clipped withs and normal without morphs.

	Clipped Withs			Without			Hyper.
Size	Offer	Attack	%	Offer	Attack	%	X^2
Medium	88	58	66	89	37	42	10.48***
Large	43	26	60	44	26	59	0.02

Table 15: Attacks by pike on normal and altered with morphs.

	Normal Withs			Clipped Withs			Hyper.
Size	Offer	Attack	%	Offer	Attack	%	X^2
Medium	30	14	47	30	18	60	1.05
Large	30	21	70	30	23	77	0.33

Table 16: Invertebrate predation on pelvic morphs (cover provided, dorsal morphs separate then combined).

	With			Without			Hyper.
Conditions	Offer	Ate	%	Offer	Ate	%	X^2
Lethocerus americanus as predator:							
small	76	34	45	73	40	55	1.50
medium	27	15	55	26	13	50	0.16
Dytiscus sp. (larvae) as predator:							
small							
5 dorsals	49	29	59	49	17	35	5.84**
6 dorsals	35	21	60	34	21	62	0.02
medium	7	3	43	7	4	57	0.27
Aeschna sp. (nymph) as predator:							
small	5	0	0	6	4	67	4.76*

Attacks (marks plus consumed) on intact fish (Table 13) shows similar results to consumed (Table 7) with the following exceptions. The between morph attack differential for the large, cover experiments is reduced to equal those for small and medium (X^2 = 0.78 cf. 0.82 and 0.85), that is, all sizes of Culaea were attacked with equal frequency. The differential for large, no cover, experiments, X^2 increased from 0.22 to 1.47, that is; larger sized prey are attacked more than smaller prey (see also the pike stomach results). Results for attacks on the altered morphs (Tables 14 and 15) parallels those for the consumed,Tables 8 and 9.

Invertebrate predation

Lethocerus americanus does not selectively prey upon either pelvic morph in the size groups considered (Table 16). Dytiscus sp. showed significant selective predation on small, five dorsal withs but no selection of either pelvic morph with six dorsal spines. Aeschna sp. showed significant selective predation on the without morphs in the one experiment conducted.

Discussion

Pike (1976 results) which are naive to stickleback spines learn to differentiate between pelvic morphs and select the least spiny (without) individuals. Such selection occurs prior to the pike's attack since no escapes (predator marks) of either morph were noted. The basis for this pre-selection is unknown; inferences from subsequent work suggests it may be behavioural differences in mobility. Pike are capable of visually discriminating the morphological difference (Ali and Anctil, 1976). It is unclear why the same pike would not select the without morph in the Whitemud Creek experiments. These prey fish were slightly larger and both morphs may have greatly exceeded some critical measurement (rather than just the with morphs - see below) or a behavioural difference between prey populations may exist. Redwater fish have historically been exposed to heavy pike predation while the Whitemud fish probably have not been preyed upon as much. Further investigation of site specific variation in the stickleback populations would clarify this point and may lend support to Nelson's (1977) independent site-specific hypothesis of the polymorphism origin.

Comparing the 1976 and 1977 Redwater results suggests a difference in the predator also occurs. Redwater pike seem better able to cope with the pelvic spines of the with morphs than do Sturgeon River pike.

The effect of the pelvic spine loss without other between morph complicating differences is shown by the clipped with/normal with experiments. The non-significant trend is selection for medium withs. There is no selection for either large morph perhaps due to the influence of size discussed below. The conclusion is that the pelvic spines do protect their owners to some extent but other factors inherent in each morph influence this to a variable degree.

Making the withs morphologically equivalent to the withouts results in significant selection against medium, clipped withs. There is no selection for either morph of the large size category.

Since there is essentially no morphological difference this selection must be due to other non-morphological differences between morphs such as behaviour. No cover vegetation is present (hence one aspect of differential accessibility is eliminated) so the postulated behavioural difference may be associated with activity either before predation (which would attract the pike) or after orientation (which would enhance completion of the predatory sequence). Other explanations are possible, for example, differences in schooling position of the morphs would result in differential selection, since pike take the fringe members of a school (Nursall, 1973) especially at low light intensities (Dobler, 1977). Information bearing on some of these postulations is presented in the behavioural section.

The observed results using unaltered prey indicates that predator-prey size ratio has an influence upon predation. Small pike (110-180 mm SL) were used in this study. In a predator which grasps, manipulates then swallows its prey whole, the maximum body depth of the prey item has been shown to be highly correlated with pike jaw width (Christiansen, 1976). These pike have a maximum jaw width of 1.5 cm; the prey used in the experiments have a total body depth (TBD) of: small with 0.70 cm, without 0.59 cm; medium with 0.92 cm, without 0.81 cm; and large with 1.14 cm, without 1.03 cm (Appendix 5). The morphs in the large category both closely approach the maximum body depth these pike are capable of handling. This coupled with the fact that the total body depth of both withs and withouts is actually a triangle between dorsal and pelvic spine tips, or dorsal and belly corners would not only make large (with respect to the pike predator) withs especially unattractive as prey items but large withouts would be unacceptable also. Additional support for this is seen in Table 9. Both large prey types - clipped with and normal with - approach the critical TBD the pike can consume so neither is selectively preyed upon. The medium prey fish do not exceed this critical TBD and selection occurs upon the least spiny form. A similar situation is shown in Table 8 (altered with/normal without) with significant selection occurring in the medium size and little in the large prey size groups.

Consequently, for the pike experiments using small prey fish, the polymorphism is at least morphologically unimportant to the pike, no fish escape and the withs are essentially equivalent to the withouts. It may also be inferred that the morphs at this size (age) are behaviourally similar (see behaviour section). For the medium size category the spine effectiveness is still not maximal (few escapes) thus there is a tendency to prey on withs which are preferred for behavioural reasons. The TBD of the large prey fish approaches or exceeds the pike's jaw width making both morphs (but withs more so) unattractive as prey items. The attacks upon the size groups do not vary with size but rather the important parameter is escapability after capture. The with morph is better able to escape hence selection may be for withouts, but this is countered by the assumed behavioural difference which favours the without morph. Thus, the selection for each morph never becomes significant in the experiments with intact prey since these two factors work in opposite directions to protect their owners. However, removing the spines results in significant selection upon the with morph (behaviourally preferred) in the medium size group. The differential escapability of the large morphs is due to the effect of the pelvic spines but other factors are influencing these results (since when presented singly the same size of prey never escaped once captured - see behaviour section).

Popova (1966) has noted that the erectile nature of spiny armament in fish has an additional advantage, in that the potential increase in size of the prey makes it less available to small predators. In the Wakomao Lake situation, the early appearance and rapid growth of spines (see introduction) would remove withs from young-of-the-year pike predation for a longer period of time than withouts. This would represent a distinct advantage to the with morph, especially early in the year, which might explain their greater frequency in the lake.

From this size selective hypothesis several predictions are possible. First, for very small pike predators the morphological difference in the morphs even at small prey sizes will be important, thus a sample of wild caught pike (or experimental pike) of a size from 5-12 cm SL will select for small without morphs (assuming no other difference between small morphs exists). Second, larger predators, that is above 20 cm SL, will select large withs for behavioural reasons only, since the spines or their absence makes no difference to these pike.

The no cover experiments attempt to make the pelvic morphs behaviourally equivalent by equalizing the accessibility of each morph. The slight difference in selectivity and attacks between the cover and no cover experiments (X^2 greater in cover for any pair-wise comparison of a size group) suggests that the morphs differentially use cover vegetation to minimize predation. Whether this postulated behavioural difference is related to association with cover or whether it is interference of vegetation in the pike's attack is not known. Attacks on each morph in cover are equal across size groups indicating that, when cover vegetation is present pike prey opportunistically on what is available. In no cover situations the attacks increase with size of the prey, thus pike select for larger prey items if they are available (see stomach section).

The morphological difference probably means nothing to invertebrate predators such as _Lethocerus_ and _Dytiscus_ which pierce and suck prey items. The observed non-selective predation of _Lethocerus_ and selection on withs by _Dytiscus_ is related to the ways these predators prey. _Lethocerus_ is strictly an ambush predator. Predation on each morph is a statistical event correlated with morph density, hence non-selective (but see general discussion). _Dytiscus_ sp. is an active, ambush-lunge predator. The morphological differences between pelvic morphs may cause differential escape speeds and thus have a small but untested influence upon the selection. However, the most pausible explanation for the observed selection is a behavioural difference between morphs pleiotropically associated with the gene determining pelvic morph (see behavioural section). Spines, both pelvic and dorsal, are used by _Aeschna_ sp. to grasp and hold _Gasterosteus aculeatus_ (T. E. Reimchen, pers. comm.). Reimchen also gives evidence that a pelvic polymorphism in G. aculeatus is partly a response to heavy dragonfly predation in which the unspined morphs are favoured. These results are opposite to those observed in the present study but small sample sizes prevent firm conclusions.

There is also a suggestion of differences between dorsal spine groups in these data, selection is upon large five dorsal spined but not on six dorsal spined withouts by pike; and upon small five dorsal spined withs but not on six dorsal spined withs by Dytiscus. The involvement of two radically different predators suggests that the difference between morphs is not morphological (but perhaps behavioural). Rigorous testing of this hypothesis may yield evidence regarding why some Culaea populations have stronger modes at six dorsal spines than at five (Lawler, 1958; Nelson, 1969); that is, this difference may also be predator related.

In summary, it is clear that two morphological factors influence pike predation in these experiments - predatory/prey size ratio and the pelvic spine condition of the prey. For small pike (four times prey length or less) the with morphs' TBD greatly exceeds some critical measurement, probably jaw width, so preference is for withouts. Both morphs escape from small predators but the withs are favoured. A larger predator whose jaw width exceeds the critical minimum does not respond to the presence of the pelvic spines, that is, to large pike the pelvic morphs are morphologically equivalent. Escapability of the morph before contact or inaccessibility will be favoured in this situation (most pike taken in the lake are much larger than the minimum size for spines to be effective) so a behavioural difference between morphs has been postulated to account for results observed in experiments.

The morphological difference in _Culaea_ makes no difference to _Lethocerus_ or _Dytiscus_ predators but may be a factor in _Aeschna_ predation. Differential predation by _Dytiscus_ sp. is attributed to a hypothesized behavioural difference(s) between morphs.

LABORATORY BEHAVIOUR EXPERIMENTS

Methods

Pike predator

All behaviour experiments were conducted at room temperature (19°C) in a large glass aquarium (49.5 cm x 38 cm x 121 cm) divided into three compartments by opaque white, removable plexiglass dividers. The tank was enclosed by a black plastic hood to restrict disturbance during observation. During experiments the room lights were off and the tank was illuminated by two fluorescent tubes mounted under the hood. Observations were made from about 0.5 m from the tank wall through a vertical slit, 15 cm long in a cardboard screen. Movements by the observer attracted a few prey fish during the initial observations but usually the fish would appear disturbed for only a few seconds. The pike also oriented to the opening for brief periods during the second set of observations.

The holding section (49.5 cm x 38 cm x 43 cm) of the tank was ungravelled and provided with a single row (4) of plastic aquarium plants (*Myriophyllum* and *Ceratophyllum*) mounted on a clear plexiglas strip. Aeration was by two airstones and filtration by an outside siphon filter. An experimental section of the same size was provided with cover along the outside, end wall (49.5 cm). A single pike was resident here between behaviour experiments. A middle section (49.5 cm x 38 cm x 15 cm) was the holding area for the pike during experiments. No airstones or filters were present in the latter two sections of the tank. Grey pea-size aquarium gravel covered the bottom of both of these sections.

Fish of the appropriate size were removed from the flow-through holding tanks and scored to pelvic and dorsal morph then put in the holding section in groups of 20 of each morph. An acclimation period of one week was allowed to control for aberrant behaviour when the fish were confronted with the transparent glass wall. Fish were fed every second day on frozen brine shrimp.

Two pike, 165 and 170 mm SL, both from the Redwater River, were used sequentially in the behaviour experiments.

All behaviour experiments were conducted with five dorsal spined, with or without pelvic morphs in three size categories: small (20-29.9 mm), medium (30-39.9 mm) and large (40-49.9 mm). All were observed individually and pelvic morphs presented in random order.

Each experimental fish was removed from the holding section, measured, rescored to pelvic morph then tipped gently into the cover vegetation of the experimental section. The fish was allowed to recuperate for one hour then 15 minutes of baseline behaviour was recorded. At the end of this period, the divider separating the experimental chamber from the pike holding chamber was lifted by an external line. The pike usually entered the experimental section quickly and a further observation period was conducted. This lasted until the prey fish was eaten or until 15 minutes had elapsed. Lifting the divider caused some reaction by the prey fish but the effect lasted only a few seconds and appeared not to affect the outcome.

The following behaviours were measured for both the baseline and predator experiments as cumulative time on an Esterline Angus 20 event chart recorder (cf. Huntingford, 1973):

a) total activity - sum of time spent active (Σ b to d).

b) jerky swim - bouts of fin movement with slow forward movement of the body typical of undisturbed fish investigating food items etc.

c) sculling - pectoral and caudal fin movements present but no forward movement of the body. A behaviour shown when the fish seems 'unsure' or 'appraising' the situation.

d) fast swim - bouts of lateral body flexions producing rapid forward motion characteristic of a disturbed or fleeing fish.

e) frozen - no fin or body swimming activity, opercular and eye movements are present; typically shown by fish which seem agitated or attempting to be cryptic. This behaviour usually occurred with the fish resting on the bottom or in vegetation but also occurred near a corner up in the water column. This behaviour is correlated with a change in colouration (see below) which strengthens the impression that it is associated with attempts at crypticity.

f) in cover - time spent associated with the cover vegetation either below or within one standard length beside or above the vegetation (includes time in vegetation).

g) in vegetation - time spent actually in contact with the plants usually by wedging the body between the rosettes of leaves.

h) dorsals erect - time the dorsal spines were fully erect.

These behaviours were expressed as percentages of the total possible time (15 minutes in the baseline and total time of experiment in the predator experiment).

During the predation experiment the following additional behaviours were recorded and expressed as minutes:

i) survival time - total time the prey fish survived with the predator present.

j) manipulation time - total time the predator manipulated captured fish before swallowing.

k) time to first orientation - the time between lifting of the divider and the first orientation of the predator to the prey.

A tape recording of the predation experiments provided information about rapidly occurring, discrete events:

l) approaches - direct movements towards the predator of more than 2 cm.

m) retreats - slow but purposeful direct movements of more than 2 cm away from the predator usually by jerky swimming.

n) jumps - rapid escapes (fast swim) away from the predator.

o) direction of swallowing by the pike was recorded as head first, tail first or unknown.

The data were analyzed as follows:

1. The percent timed data (variables a-h) were normalized by the angular transformation (Rohlf and Sokal, 1969, p. 129). Timed data for variables (i-k) were expressed in minutes. Means and

standard deviations were computed (Appendix 6, Table 49). Means were transformed (a-h) back to percentages of real time for Table 17.

2. A univariate factorial anova was calculated for each of the timed behaviours (a-h). The three factors used were pelvic morph, experiment type and size of prey fish. An additional two factor (morph and size) anova was applied to behaviours (i-k).

3. A multivariate factor analysis was conducted on variables b-g, m and n by morph and size. For this analysis retreats and jumps were expressed as normalized percentages of the total for that morph. In the present case, the factor analysis was used first as a data reducing and variable patterning technique and second to test the hypothesis that, simultaneous contributions from the measured variables might result in a between morph difference in behaviour which would account for the observed differential predation by pike (see laboratory predation experiments).

4. Between morph or within morph size differences in behaviours l-o were tested by normal, row X column chi-square with Yates' correction for continuity applied as necessary.

Chi-square values were calculated for goodness of fit to the expected frequencies. Descriptive statistics (mean and standard deviation), factorial anovas and the factor analysis were calculated by the University of Alberta computer using the Statistical Package for the Social Sciences (SPSS) program. The subprograms used were, respectively, Condescriptive, Anova and Factor (Nie et al., 1975). For Anova, the classical method of dealing with unequal cell frequencies was used. For Factor, the principal components method without iteration (PA1) was used, followed by Varimax rotation.

Dytiscid Predator

The only standardized behaviour experiments conducted with invertebrate predators were done using dytiscid larvae. The experiments were conducted in a glass aquarium (30 cm x 30 cm x 60 cm) at room temperature (21°C). Oyster shell gravel covered the tank bottom and aeration was by two small bubble-up charcoal filters in the tank corners. Six artificial plants (*Myriophyllum* and *Ceratophyllum*) were placed in half (either left or right) of the tank. Illumination was by a single 15 watt fluorescent tube.

Three fish of each morph were measured (SL) then gently placed in the tank. An acclimation period of 2-3 hours was allowed then three dytiscid larvae were added to the tank. After five minutes (during which time the behaviour of the prey fish appeared to return to normal), a one-half hour observation period was conducted. The next morning (15 hours later) a second one-half hour observation period was carried out. The observer sat in a darkened room about one m from the tank. Five replicates of each experiment using small, five dorsal spined fish were conducted. The following behaviours were recorded: numbers of approaches by each morph and the closest distance of each approach (measured as SL units and converted to linear units). Morphs were differentiated by clipping the dorsal fins of one or the other alternately in the experiments.

Row by column chi-square was calculated for the approaches by the morphs. An unpaired t value was computed for mean distance of approach by

$$t = \frac{\overline{X}_1 - \overline{X}_2}{\frac{s_1^2}{n_1} - \frac{s_2^2}{n_2}}$$

where $\overline{X}$ = mean,
s^2 = variance, and
n = number of observations,

then tested for significance from tabled values in Rohlf and Sokal (1969, p. 159).

Results

Stickleback Behaviour when Confronted with a Predator

Culaea's first reaction to a pike predator was cessation of normal activity then sinking in the water and quiet sculling. During this period the normal pale, uniform colouration of the fish became broken up by dark saddles of pigment alternating with pale patches. This enhancement of contrast resulted in the fish being more cryptic against the appropriate background (vegetation or detritus). Fish on a grey gravel background became more difficult for a human observer to see. Sudden movements or orientations by the pike at this point resulted in the stickleback seeking cover usually by a rapid jump. When entering cover the fish either hid behind or under stalks of vegetation or actually inserted itself between rosettes of leaflets of several stalks. Once in cover the fish froze, and used only small eye movements to keep the predator in sight and restricted opercular movements. If the predator was observed while the prey fish was far from cover, it would also freeze on the spot, either on the bottom or in a corner up in the water column. If the predator came very close during this frozen period the opercular and eye movements may be completely halted. Such freezing was maintained for long periods of time especially if the pike was close and oriented to the prey. This freezing behaviour was adaptive in that, even if the pike was oriented to the prey, it would eventually lose interest and turn away if no movement to stimulate the lunge was forth-coming. The frozen behaviour was often maintained as long as the pike was in view. Spine erection in this population of _Culaea_ when the predator was near was restricted to dorsal spines only (with morphs included). The range of behaviour in _Culaea_ varied greatly with the individual (a function of past experience?) as well as with the age of the fish. Small _Culaea_ seemed not to recognize the potential danger of the pike and sometimes approached to within one or two centimeters then, if they had not been eaten, backed away (retreated) slowly. Small sticklebacks often showed ignoring behaviour during which they carried on their normal activities totally oblivious to the pike.

The above description applies to sticklebacks confronted with a predator much larger than themselves and of obvious potential danger. _Culaea_ did not recognize the invertebrates as potential predators and readily approached any movement by objects of a similar or smaller size than itself. The stickleback would swim jerkily toward the object that moved to within a few centimeters, hesitate then back away. Objects which continued to move were followed for a few centimeters then ignored. Attempts at contact by the stickleback such as nipping of projections or prominences might be made. Objects which moved after being investigated were re-investigated. If the object is large (such as Lethocerus) the approach was made with dorsal spines erect (pelvics not erect in with morphs). Immobile objects, even if in clear view were not investigated until they moved; however, sticklebacks would swim very close to them (e.g. between the outstretched forelegs of Lethocerus). Capture of one individual by an invertebrate predator induced conspecifics who witnessed the capture to avoid that predator for some time after the attack but this response eventually waned. The behaviour seemed consistent with all ages but this was not rigorously investigated.

Culaea reacts in the typical gasterosteid fashion once captured by a predator - erection and locking of all spines (pelvics also in with morphs) occurred and the body was held rigid. Attempts at wrenching the body free may be made especially if the predator was an invertebrate but these were usually unsuccessful. With morphs probably had a slight advantage due to their extra spines during manipulation and swallowing by pike (see predation experiments section).

Pike Experiments

Three comparisons of timed behaviour are possible: between morph, within morph between experiment type (effect of the predator) and across the size categories. Means of timed behaviours are given in Table 17 and Figures 2 and 3.

No triple factor interaction (Table 18) is significant. Morph by size interaction for the variables cover and survival time is significant and the experiment type by size interaction for the variables total activity and cover approach significance at $p = 0.05$.

Table 17: Real mean percentage[1] of time spent in various activities.

Behaviour	Baseline Experiment						Predator Experiment					
prey size	small		medium		large		small		medium		large	
morph	with	w/o	with	w/o	with	w/o	with	w/o	with	w/o	with	w/o
Total activity	96.4	92.7	64.4	68.0	76.7	91.8	90.4	84.6	3.7	36.0	41.3	29.5
Jerky swim	55.3	34.0	35.9	42.5	51.0	77.5	15.0	17.2	0.3	2.2	4.1	2.9
Scull	15.2	25.7	10.7	25.4	24.6	6.2	39.6	38.4	1.8	16.7	23.7	28.6
Fast swim	6.6	20.8	0.0	0.0	0.5	0.0	4.7	4.9	0.1	0.3	0.1	0.6
Frozen	3.6	7.3	35.5	32.1	19.2	8.1	8.2	8.1	96.4	68.1	58.7	70.7
In cover	17.6	24.0	78.2	43.2	38.3	42.2	28.6	2.0	97.1	68.2	58.8	89.7
In vegetation	1.3	0.0	0.9	1.2	0.2	0.1	14.7	0.0	16.3	9.6	2.2	10.4
Dorsals erect	11.7	17.5	50.7	60.1	21.9	55.9	31.3	27.0	95.3	81.2	48.5	95.2
Survival time[2]							2.9	3.0	12.9	8.5	5.4	7.5
Manipulation[2]							0.0	0.0	0.5	0.1	0.6	0.4
1st orientation[2]							1.4	0.6	5.1	7.6	4.3	6.1
number	14	12	15	15	15	15	14	12	15	15	15	15

1. Computed from normalized means in Appendix 6, Tables 49 and 50, using Rohlf and Sokal (1969, p.129)

2. Expressed as real time in minutes

w/o = without pelvic morph.

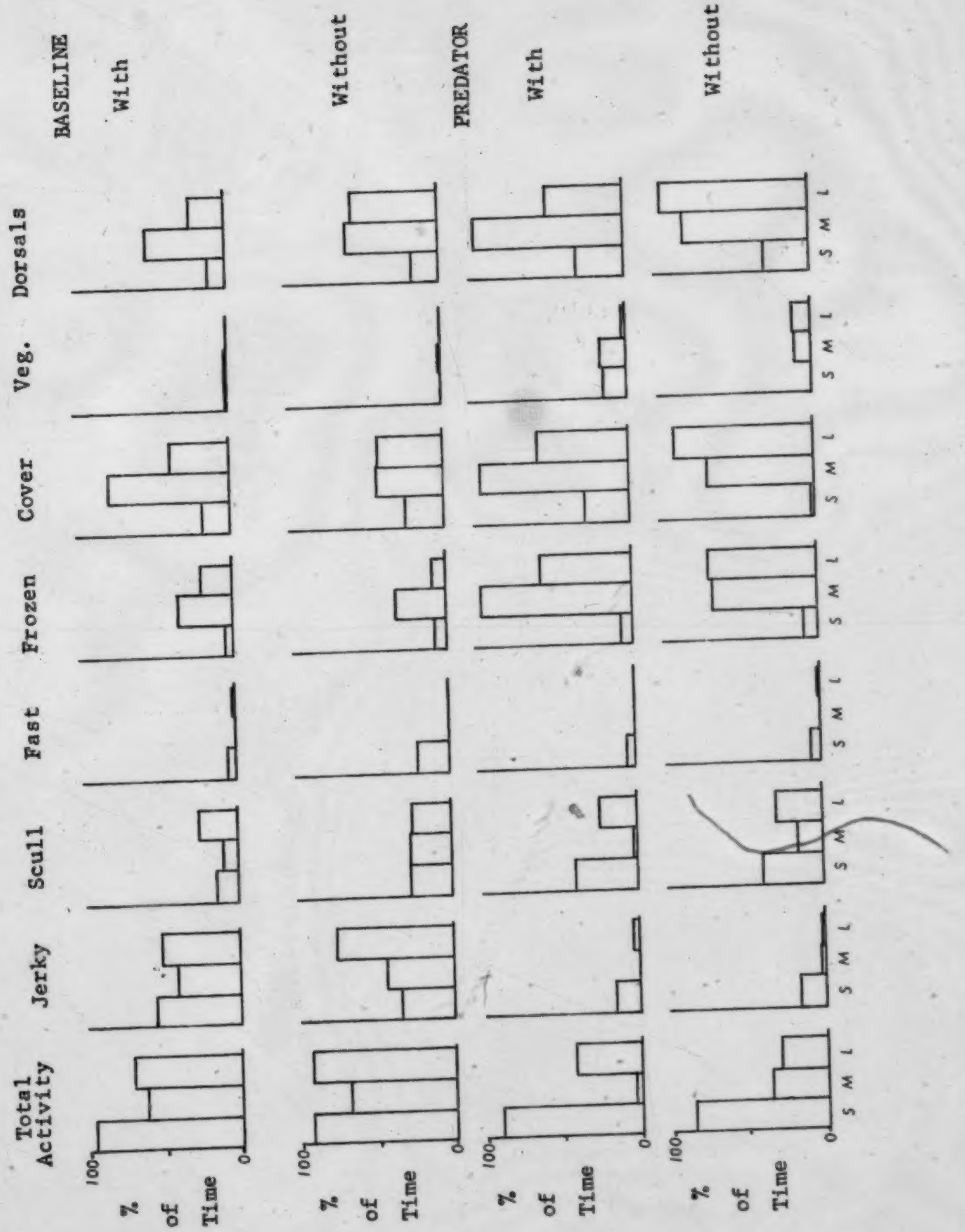
Table 18: Significance values from ANOVA test, from the normalized mean percents of Appendix 6, Table 51 ($p \leqslant 0.05$ was taken as significant).

Behaviour	Main Effects			Two-way Interactions			Three-way Interaction
	Morph	Exp. Type	Size	M. X Exp.	M. X Size	Exp. X Size	
Total activity	0.44	0.00	0.00	0.93	0.35	0.08	0.24
Jerky swim	0.58	0.00	0.09	0.86	0.51	0.10	0.35
Scull	0.59	0.12	0.01	0.78	0.44	0.25	0.40
Fast swim	0.88	0.69	0.00	0.41	0.95	0.81	0.85
Frozen	0.40	0.00	0.00	0.11	0.75	0.42	0.27
In cover	0.16	0.02	0.00	0.74	0.01	0.06	0.15
In vegetation	0.69	0.01	0.05	0.78	0.40	0.18	0.53
Dorsals erect	0.14	0.00	0.00	0.52	0.11	0.18	0.66
Survival time	0.99	--	0.00	--	0.01	--	--
Manipulation	0.13	--	0.00	--	0.47	--	--
1st orientation	0.6	--	0.00	--	0.77	--	--

M = morph

Exp. = experiment type

Figure 2: Time spent by pelvic morphs, withs and withouts, in various behaviours. S = small, M = medium, L = large size of prey; veg. = vegetation.


Total Activity
Jerky
Scull
Fast
Frozen
Cover
Veg.
Dorsals
BASELINE
With
Without
PREDATOR
With
Without
% of Time
100
0
S M L

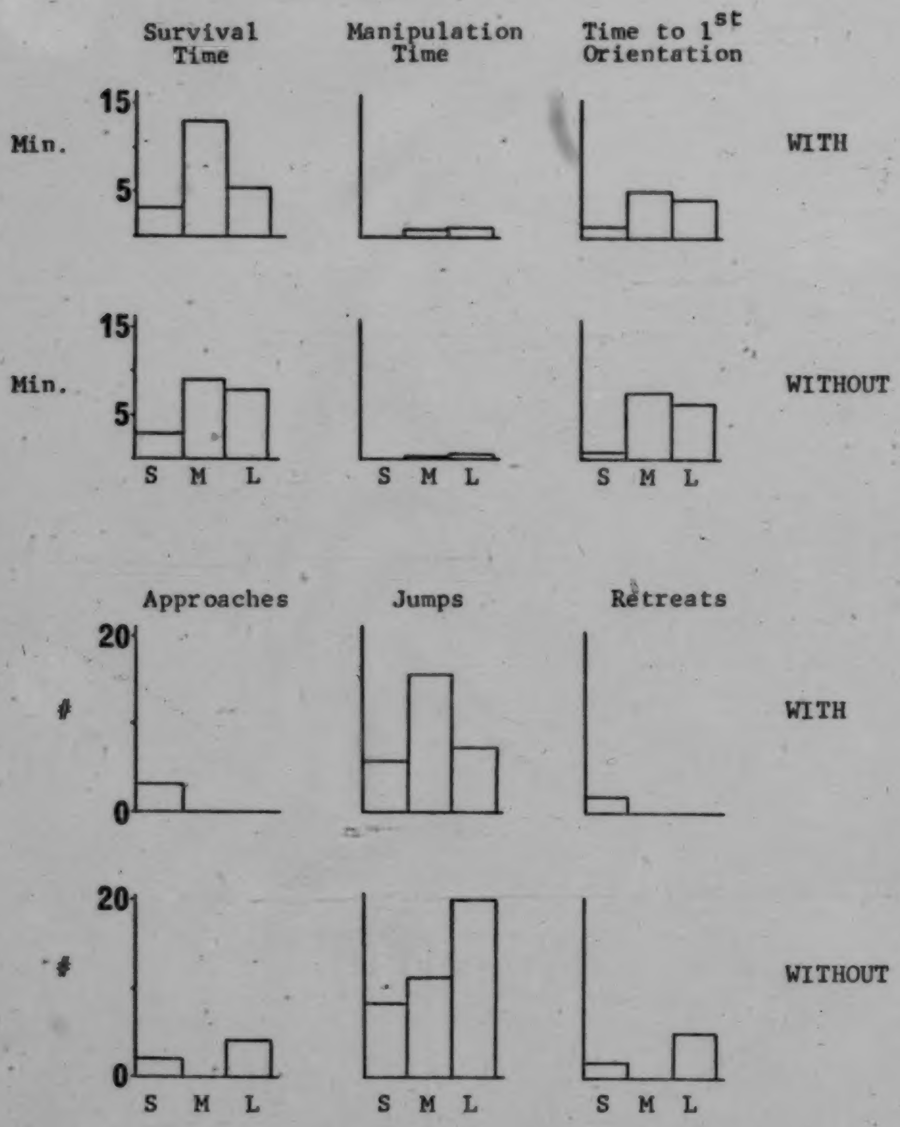


Figure 3: Behaviour of Culaea during pike predation. Min. = time in minutes; S = small prey size, M = medium size and L = large size.

All other two-way interactions are non-significant. No significant difference between the pelvic morphs (main effect) exists in any of the timed behaviours. It is clear that virtually all the variation in the data is due to the main effects of experiment type and size.

Both morphs of all size groups show very significant changes in all behaviours, except scull and fast swim, between experiment types (Table 18). The addition of the predator caused a decrease in total activity especially jerky swimming and a corresponding increase in time frozen, time in cover and vegetation, and time with the dorsal spines erect. These changes in the mean time usually were quite large except in the small size category where they may even be reversed (Table 17 and Figure 2).

The change of behaviour with size is more complicated. Activity variables (total activity, jerky, scull or fast) for both morphs in both experiment types either decrease with increasing size or are the lowest in the medium size group (Figure 2). Time spent in behaviours associated with hiding or defence (frozen, cover, vegetation and dorsals) generally increase with size or more often peak in the medium size category. These effects when noted are more pronounced in the with morph and in the predation experiments but all are significant at p = 0.05 or closely approach it (Table 18).

Behaviours associated with the predator presence show similar trends (Table 17 and Figure 3). Survival time and time to first orientation peaks for the medium size group. Manipulation time shows a steady increase with size.

The only discrete behaviour (Table 19) which shows a significant difference between morphs was that large withouts jump more often than withs. Small and medium fish jump about the same number of times and withs jump slightly farther than withouts. Small withs and withouts approached the pike equally often, medium fish never approached and large withouts approached several times from behind vegetation but this difference is not significant. Overall, withouts tend to retreat more often but this is not significant for any size group. Both morphs retreat about the same distance.

The factor analysis of all behaviours which may be important during predation, and subsequent simplifications, have reduced the results to five underlying factors which account for 73.1% of the total variance in the data. The absolute value of the variable loading is a measure of the input of that variable to the underlying factor; thus a high loading, either positive or negative, implies a large contribution by that variable. Variable loadings also represent correlations between variables thus high loadings on the same factor by two or more variables implies a good correlation (either positive or negative) between variables. A fuller description of the methods and interpretations of factor analysis data is given in Appendix 6.

Factor 1 (Table 20) has large positive loadings for size, frozen, cover and vegetation and a negative loading for fast swimming. Factor 2 has a high positive loading for frozen and large negative loading for sculling. Factor 3 is an underlying behaviour axis positively loaded for jerky swimming and retreat and negatively for frozen. Factor 4 is highly loaded for jumps and negatively for

Table 19: Differences in morphs in discrete behaviours. Goodness of fit X^2 to a 0.50:0.50 or 0.33:0.33:0.33 expectation; w = with morph, w/o = without morph.

Behaviour	Prey Fish Size	Morph	#	Mean Distance (cm)	X^2 between morph (within size)	X^2 within morph (by size)
Approaches	small	w	3	4		
		w/o	2	4	0.00_1	
	medium	w	0	-		
		w/o	0	-	0.00	
	large	w	0	-		
		w/o	4	5	2.26_1	
	all	w	3	4		2.75_1
		w/o	6	4	0.44	2.25_1
Jumps (= successful escapes)	small	w	6	34		
		w/o	8	23	0.28	
	medium	w	16	23		
		w/o	11	20	0.92	
	large	w	7	35		
		w/o	20	35	6.26**	
	all	w	29	31		6.23*
		w/o	39	26	1.46	5.999*
Retreats	small	w	2	11		
		w/o	2	5	0.00	
	medium	w	0	-		
		w/o	0	-	0.00	
	large	w	0	-		
		w/o	5	18	3.20_1	
	all	w	2	11		1.09_1
		w/o	7	12	1.78_1	3.53_1

Table 20: Varimax rotated factor matrix on behaviour data from pike predation experiments (from Appendix 6, Table 54; final solution, second simplication = rounded off to nearest 0.01 and loadings less than 0.3 absolute value are deleted).

Variable	Factor 1	2	3	4	5
Morph					0.99
Size	0.67				
Jerky			0.74		
Scull		-0.97			
Fast	-0.72				
Frozen	0.41	0.79	-0.33		
In cover	0.72				
In vegetation	0.45			-0.30	
Retreat			0.85		
Jumps				0.90	
% of original variance	27.7	14.0	11.0	10.4	10.0

vegetation. The final factor is heavily loaded for morph differences but it accounts for the least amount of total variance. The relative importance of a factor is given by the proportion of total variance for which that factor accounts (Table 20). The importance of these factors is given by their order, 1 > 2 > 3 > 4 > 5.

After capture, the direction of swallowing of each morph does not vary (Table 21) for any size group. However, significantly more large fish of each morph are swallowed head first.

Dytiscid Experiments

Neither morph (Table 22) approaches the dytiscid predator more often (initially withs approach more, later withouts approach more but this is non-significant in both cases). However, for the 73 approaches in which the closest distance between stickleback and dytiscid was noted it is clear that withs approach significantly closer (Table 23) thus placing themselves in a more vulnerable position with respect to potential predation.

Discussion

The Defences of Sticklebacks

Edmunds (1974, p. xiv) takes a holistic approach to animal defence since "most prey species have a variety of predators and most predators can eat a variety of prey species, so the defensive adaptations of animals are usually directed at several different predators." He further defines defensive adaptations as those which reduce (but not necessarily eliminate) the chances of a successful attack by

Table 21: Direction of swallowing of pelvic morphs. Goodness of fit X^2 to 0.50:0.50 or 0.33:0.33:0.33; abbreviations as in Table 19.

Direction Swallowed	Prey Fish Size	Pelvic Morph	#	X^2 between morph (within size)	X^2 within morph (by size)
Head first	small	w	6		
		w/o	7	0.08	
	medium	w	0		
		w/o	2	0.50_1	
	large	w	6		
		w/o	9	0.60	
	all	w	12		4.18*
		w/o	18	1.20	4.34*
Tail first	small	w	6		
		w/o	4	0.40	
	medium	w	4		
		w/o	7	0.82	
	large	w	4		
		w/o	1	0.80_1	
	all	w	14		0.59
		w/o	12	0.15	3.13_1
Unknown	small	w	0		
		w/o	0		
	medium	w	1		
		w/o	1		
	large	w	2		
		w/o	1		

Table 22: Approaches of sticklebacks to Dytiscid predators.

Experiment Type	Morph	# of Approaches	χ^2
(b) Immediate Observation	with	37	
	without	25	2.32
(c) Observation after 15 hours	with	10	
	without	16	1.89
Both	with	47	
	without	41	0.20

Table 23: Closest distances approached to Dytiscid predators.

	Distance Approached (cm)								
Morph	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0
with	7	6	18	1	9				
without		3	14		10		4		1

	Approach Distance			
Morph	#	Mean	S.D.	Var.
with	41	1.99	0.6660	0.4436
without	32	2.61	0.8774	0.7699

$t = 3.336^{***}$ ($0.001 < p < 0.005$ at 71 df)

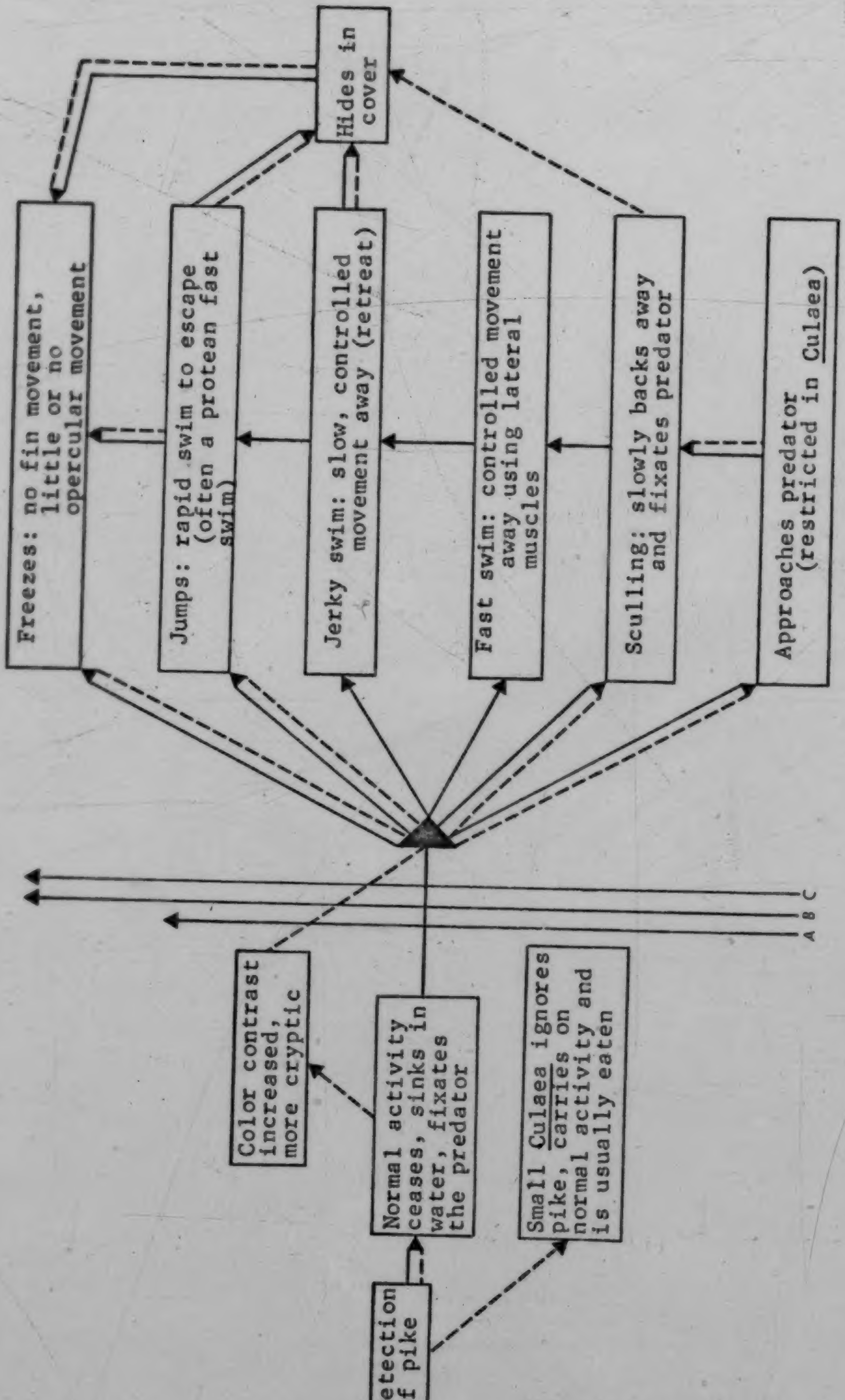
S.D. = standard deviation, var. - variance = (standard deviation)^2

another animal.

Anti-predator defences may be divided into two types (Edmunds, 1974). Primary defences operate regardless of whether or not a predator is in the vicinity and function to decrease the chances of encounter with the predator, for example, aposematism and crypsis. Secondary defences function to increase a prey animal's chances of escape when it encounters a predator. Usually the first response of the prey is an exaggeration of a primary defence, especially if the prey detects the predator first (e.g. enhancement of cryptic colouration). Next an assessment of the situation usually occurs during which a course of action is decided upon. Such a course depends upon the predator, its proximity and the position in the predatory sequence. The resulting action may be either slow controlled movement away or protean defensive flight if the predator is pursuing. The flight sequence often leads the prey to cover, where it may remain depending upon crypsis, or to a diematic behaviour such as threat display. Prey reaction to capture may be thanatosis (death feigning), deflection of attack, or retaliation by the prey's defensive mechanisms. Prey organisms usually have more than one method of defence at their disposal and any single structure or behaviour may accomplish several tasks (Edmunds, 1974).

The behavioural defensive repetoire of Gasterosteus aculeatus has been documented by several workers (Benzie, 1965; Hoogland et al., 1957) and summarized by Wootton (1976). This work is presented in Figure 4 in the general framework of Edmunds' (1974) description. The present work on Culaea was fitted into this

Figure 4: Stickleback behaviour when confronted with a piscivorous predator. ⟶ *Gasterosteus aculeatus*; after Benzie, 1965; Hoogland et al., 1957; Wootton, 1976. ⇢ *Culaea inconstans*, present study. ⟹ both species. A, increasing frequency of fin beats and opercular movements. B, increasing tendency for dorsal spine erection. C, increasing proximity of the predator.


Detection of pike
Normal activity ceases, sinks in water, fixates the predator
Color contrast increased, more cryptic
Small Culaea ignores pike, carries on normal activity and is usually eaten
A B C
A B C
C
Freezes: no fin movement, little or no opercular movement
Jumps: rapid swim to escape (often a protean fast swim)
Jerky swim: slow, controlled movement away (retreat)
Fast swim: controlled movement away using lateral muscles
Sculling: slowly backs away and fixates predator
Approaches predator (restricted in Culaea)
Hides in cover

description where relevant.

Culaea behaves similarly to *Gasterosteus* but with some important exceptions, notably, the colour change and the increased tendency to show escape or avoidance rather than investigative (approach) behaviour. These behavioural differences agree well with the established information about *Culaea*, that is, it "is a skittish, shy fish compared with *Gasterosteus* or even *Pungitius*." (Wootton, 1976, p. 293).

The long, stout spines of *Gasterosteus* are broken by piscivorous predators before the fish is swallowed, usually by spitting the fish out then sucking it back in (Moodie et al., 1973; T. E. Reimchen, pers. comm.) - a situation which provides ample opportunity for escape. The weak spines and unprotected body of *Culaea* suggest that once it is captured it is easily swallowed by predators much larger than itself and rarely escapes. Laboratory data and field work substantiates this: of over one hundred pike predations observed in the lab no fish escaped once it had been held in the pike's jaw; however several fish escaped by eluding the pike's lunge; and only one of several thousand lake fish examined shows predation marks (but see predation experiments section).

Culaea's spines seem especially ineffective against a large predator such as a pike which mouths its prey. Its spines serve no function against invertebrate predators. Hence, the optimal defence for *Culaea* seems to be one of avoiding the predatory situation as much as possible by behavioural means.

Pike Experiments

The change in behaviour of sticklebacks upon introduction of a pike has obvious adaptive value since pike orient to and stalk moving prey items. The prey fish of both morphs are aware of the potential danger the pike represents so they all respond by making themselves less available or obvious by decreasing movements, increasing crypticity and association with cover vegetation. The turning away of the predator from an immobile stickleback and the interference of cover vegetation (predation experiments section and Christiansen, 1976) point out the value of these behaviours.

Similar behaviour changes with increasing size and the seeming ignorance by small prey of the danger that a pike represents may reflect a learning process by the prey or it may be a response to different selective pressures operating at different times in the stickleback's life. Small prey items are less preferred by pike (see stomach section). It is unclear why the most adaptive (in the present frame of reference) behaviours are shown by the medium size group of sticklebacks. This may be a reflection of the intensity of selection upon the medium size group. Small prey are more subject to invertebrate predation, large prey more to pike predation but medium size sticklebacks may be subject to both types of predators so their defensive behaviour is expressed to a greater degree. Other explanations are possible; for example, small prey may be below a size threshold for inducing attack by pike and large prey may be too rare or too difficult to capture due to better developed avoidance behaviour.

Both pelvic morphs respond to the pike's presence in similar ways. The more retreats and jumps by withouts, although not necessarily adaptive in a confined, experimental environment most certainly are in the lake situation, especially considering that the predator has many other prey items to distract him.

Huntingford (1973, 1976) adequately points out that the factors derived by factor analysis do not indicate the existance of underlying biological entities nor does the variable correlation reflect a common internal cause. However, factors with high loadings for a number of variables which on independent evidence are believed related may be tentatively labelled as biological entities.

For these data, Factor 1 with high positive loadings for size, frozen, cover and vegetation and a negative loading for fast swim would indicate an axis of escape from a predatory situation by not creating a stimulus for orientation or attack by the pike. Intuitively, given that the pike is primarily a visual predator and that sticklebacks in Wakomao Lake will be eaten, the best defence for both morphs is crypticity (immobility in cover vegetation). The loading for size would indicate that this tendency increases with size (age?) and may reflect a greater awareness of the pike's potential danger as a predator from an evolutionary sense (behavioural adaptation to different selective pressures). This increased tendency for cryptic behaviour may also be a learned effect expressed as fish grow older. Factor 2 also loads in this direction. Together these account for 41.7% of the total variance indicating the heavy reliance of the sticklebacks upon this method for escape from predation.

Active escape, either by slow retreat (Factor 3) or fast jumps (Factor 4) accounts for 21.4% of the total variance. The difference between these two percentages reflects the evolutionary significance (and relative success) of these methods of escape. That is, Culaea is a shy, retiring fish relying more on behavioural than morphological adaptations to minimize predation (Wootton, 1976).

Factor 5 is the underlying axis concerned with morph variability. Since it accounts for 9.99% of the total variance, the conclusion is that overall there is no large behavioural difference between morphs with respect to a pike predation situation, that occurs in a confined, experimental setup. In these experiments, the relative morphological advantage of either pelvic morph seems to be overshadowed by the behavioural advantage. Even though most observed differences in behaviour were statistically non-significant they nevertheless probably are biologically meaningful in that they contribute to some differential morph survivability (withouts survive more in situations involving pike predators).

Intraspecific comparison of populations responding to different selective pressures has yielded valuable insights into the role of behaviour in anti-predator defence (Liley and Seghers, 1975; Seghers, 1974a,b). A similar comparative study on Culaea populations representing the spectrum between both monomorphic extremes (100% withs and 100% withouts) could yield similar comparative information of value in elucidating the effects of different predatory regimes.

The effect of larger prey size on the pike predator, may be seen in the direction of swallowing and manipulation time (see also predation experiments). As the prey fish of both morphs approach or exceed the minimum critical TBD the pike in these experiments can handle (see Appendix 5), more manipulation time is required to turn the prey items head first for swallowing. The absolute (significant) difference in the means of manipulation time is small but not all prey fish require turning before swallowing. The greater manipulation time and turning of the prey allows for a greater chance of escape by large fish which agrees well with the observed trend in the laboratory predation experiments.

Dytiscid Experiments

Dytiscids were characterized as ambush-lunge predators making short (up to 2 cm) grabs at prey items which venture too close. The difference in approach distance by the pelvic morphs clearly puts the with morph at a disadvantage with respect to the without morph, since the success rate of dytiscids is likely to be greater upon prey which approaches closer.

Subtle behavioural differences between morphs such as that shown during dytiscid predation may be expected to be very important during insect predation. The problem of recognition and experimental pursuit of such minute differences is obvious. In a similar sense, minute ecological differences not investigated such as microdistribution of morphs within and out of vegetation beds in the lake situation may be the determining factors for selective predation by the insect predators in the wild. Despite the gross indication that morph distribution is homogeneous, subtle influences on morph availability to the predators will greatly affect predation in the lake.

In summary, with respect to both pike and dytiscid predators, the without morphs have slight behavioural advantages relative to the with morphs. These behavioural differences support the postulations of the laboratory predation experiments section, that is, withs are selectively preyed upon by dytiscids and pike (especially if despined in the latter case). However, considerable individual variation in behaviour and the specifics of each predatory situation confounds the expected outcome of predation events.

FIELD COLLECTION OF PIKE STOMACHS

Methods

A gillnetting program was conducted on the southeast portion of Wakomao Lake (Appendix 1, Figure 7) to ascertain the direction and degree of any selective predation which wild northern pike may show for the pelvic morphs or dorsal spine classes. Gillnets of a variety of mesh sizes (38, 52, 76, 89 mm stretched mesh) were set in and around aquatic macrophyte beds usually from early or mid-morning until noon. Standard length was taken, then stomachs were removed and preserved in 10% formalin.

Fish prey items in the stomach contents were analyzed and scored as to frequency of occurrence. Seven categories of stickleback prey were established: unidentified _Culaea_, unidentified withs, unidentified intermediates, unidentified withouts, withs, intermediates and withouts. The latter three were the only confirmed morphs, since to be included here the visceral cavity and one pectoral fin had to be virtually intact. Individuals not meeting these criteria were classed as closely as possible to the unidentified groups. Statistical comparison of pelvic morphs involved only these confirmed groups. The prey sticklebacks, when possible, were also scored to dorsal spine category and standard lengths were taken. These 'prey' population parameters were then compared to the same parameters taken from a sample from the lake.

The prey stickleback population from 40 pike, netted between 5 August and 18 August, 1976 was compared to a dipnet sample of lake stickleback taken on 18 August, 1976.

During 1977, 121 pike were collected from 20 July to 19 August and the prey sticklebacks compared to a composite dipnet sample taken in four subsamples spanning the stomach collection period (July 20, 28; August 11, 18).

Stomach and lake Culaea samples were compared statistically as follows. Pelvic morph and dorsal spine frequencies were compared by goodness of fit chi-square with expected frequencies derived by:

$$\frac{\text{\# of that morph in lake sample}}{\text{total in the lake sample}} \times \text{total } \underline{\text{Culaea}} \text{ in stomachs.}$$

A value for electivity (E) for each morph was obtained using the formula (Ivlev, 1961):

$$E = \frac{s - b}{s + b}$$

where s = percent representation of item in stomach, and

b = percent representation of item in lake.

This index ranges from -1 (complete avoidance of the item), through 0 (no selectivity) to +1 (complete selectivity for the item). Since the index represents only relative values for the particular food items only comparisons between morphs are valid. Pelvic morph frequencies in pike stomachs were divided into small (< 29.9 mm SL), medium (30-39.9 mm SL) and large (> 40 mm) groups and these compared to lake morph frequency of corresponding size groups. In all cases minimal statistical significance was taken as $p = 0.05$ from tabled values.

Additionally, the standard lengths of the prey (confirmed and unconfirmed prey fish) and representative lake samples were grouped into 5 mm categories and plotted as relative (percent) frequency histograms. Statistical comparison was by the Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf, 1969, p. 573) of the stomach sample to the expected lake sample frequency. Minimal statistical significance was conservatively taken as $p = 0.01$ from values in Rohlf and Sokal (1969, p. 249).

Results

Table 24 compares pelvic morph frequencies (all lengths combined) from pike stomachs to those observed in the lake collections. For both sampling years combined there is a significant difference in morph frequency. With morphs are over represented, intermediate morphs equally represented and without morphs under represented in the pike stomachs. This trend is observable in each year except for variation in the intermediates in the stomachs (fewer than expected in 1976, more than expected in 1977). Comparison of electivity indices indicates slight positive consumption of with and intermediate morphs and strong negative consumption of the withouts. That is, the observed frequencies are due primarily to a paucity of without morphs in the pike stomachs rather than an excess of withs or intermediates.

It is evident from Table 25 that the difference in morph frequency between the stomach and lake samples is due primarily to differential predation upon the small and large size groups. High negative electivity indices indicates the withouts, as before, are preyed upon much less than expected, especially in the large size

Table 24: Pelvic morph frequencies in pike stomachs compared to frequencies in the lake.

Year	Morph	Frequency In Lake (%)	Frequency In Stomachs (%)	Electivity Index
1976	with	324 (67.9)	60 (83.3)	+0.102
	intermediate	42 (8.8)	4 (5.6)	-0.173
	without	111 (23.3)	8 (11.1)	-0.355
	Total	477	72	
	$X^2 = 7.97$ $(0.01 < p < 0.025)$			
1977	with	520 (72.7)	40 (75.5)	+0.019
	intermediate	44 (6.1)	6 (11.3)	+0.308
	without	152 (21.2)	7 (13.2)	-0.228
	Total	716[1]	53	
	$X^2 = 3.94$ $(p < 0.1)$			
Both	with	844 (70.7)	100 (80.0)	+0.062
	intermediate	86 (7.2)	10 (8.0)	+0.053
	without	263 (22.1)	15 (12.0)	-0.296
	Total	1193	125	
	$X^2 = 7.36$ $(p < 0.025)$			

[1] Composite of four samples; 77-14-a, 77-16, 77-19-i, 77-20-f.

Table 25: Pelvic morph frequency in stomachs and lake samples for each size group of Culaea (both years combined).

	Lake Sample			Stomach Sample			
Pelvic Morph	Mean SL (mm)	Frequency	%	Mean SL (mm)	Frequency	%	Electivity Index
Small (15-29.9 mm)							
with	23.5	587	71.1	24.7	51	83.6	+0.081
intermediate	23.7	51	06.2	27.3	2	03.3	-0.305
without	23.8	187	22.7	26.3	8	13.1	-0.268
Total		825			61		
$X^2 = 4.61$ ($P \cong 0.1$)							
Medium (30-39.9 mm)							
with	34.1	227	71.1	35.8	28	77.8	+0.045
intermediate	34.6	29	09.1	33.9	4	11.1	+0.099
without	33.8	63	19.7	36.6	4	11.1	-0.279
Total		319			36		
$X^2 = 1.74$ ($p \cong 0.5$)							
Large (40+ mm)							
with	44.2	30	61.2	49.5	20	74.1	+0.095
intermediate	44.8	6	12.2	48.4	4	14.8	+0.096
without	43.0	13	26.5	45.7	3	11.1	-0.409
Total		49			27		
$X^2 = 5.33$ ($0.05 < p < 0.06$)							

category.

Two distinct size (length) groups of pike were taken, Table 26 compares the observed pelvic morph frequencies in small (18-27 cm SL, young-of-the-year?) and large (31-64 cm SL, older than one year) pike. Although small sample sizes make statistical comparison tenuous it is clear that morph selectivity does not depend upon size of predator, at least in this size range (18-64 cm).

The frequency of dorsal spine classes (Table 27) in pike stomachs is not different from that observed in the lake.

Figure 5 shows the standard length (SL) of prey and lake sticklebacks for 1976 and 1977 samples combined. For each morph, as well as all morphs combined, there is statistically significant more predation upon the larger size groups of Culaea. In some cases, predation occurs on individuals larger than those observed in the shoreline comparison collections. The same trends are seen in the data for each year individually (Appendix 7, Table 58).

Figure 6 compares the distribution of prey lengths in small and large pike predators for 1976 and 1977 combined. There is a just significant ($p = 0.01$) difference arising primarily from the difference in the 20-24 mm length class and a slight bimodality in the prey lengths from large pike.

In addition to noted trends of prey consumption, qualitative information on pike predation in Wakomao Lake was obtained. Sticklebacks comprised 98.1% and 53.8%, respectively for 1976 and 1977, of the identifiable prey items despite the abundance of fathead

Table 26: Pelvic morph frequencies in small and large pike predators.

Year	Morph	# In Small Pike (18-27 cm SL)	# In Large Pike (31-64 cm SL)
1976	with	58	2
	intermediate	4	0
	without	8	0
	N of pike	38	2
1977	with	12	28
	intermediate	2	4
	without	1	6
	N of pike	26	95
Both	with	70	30
	intermediate	6	4
	without	9	6

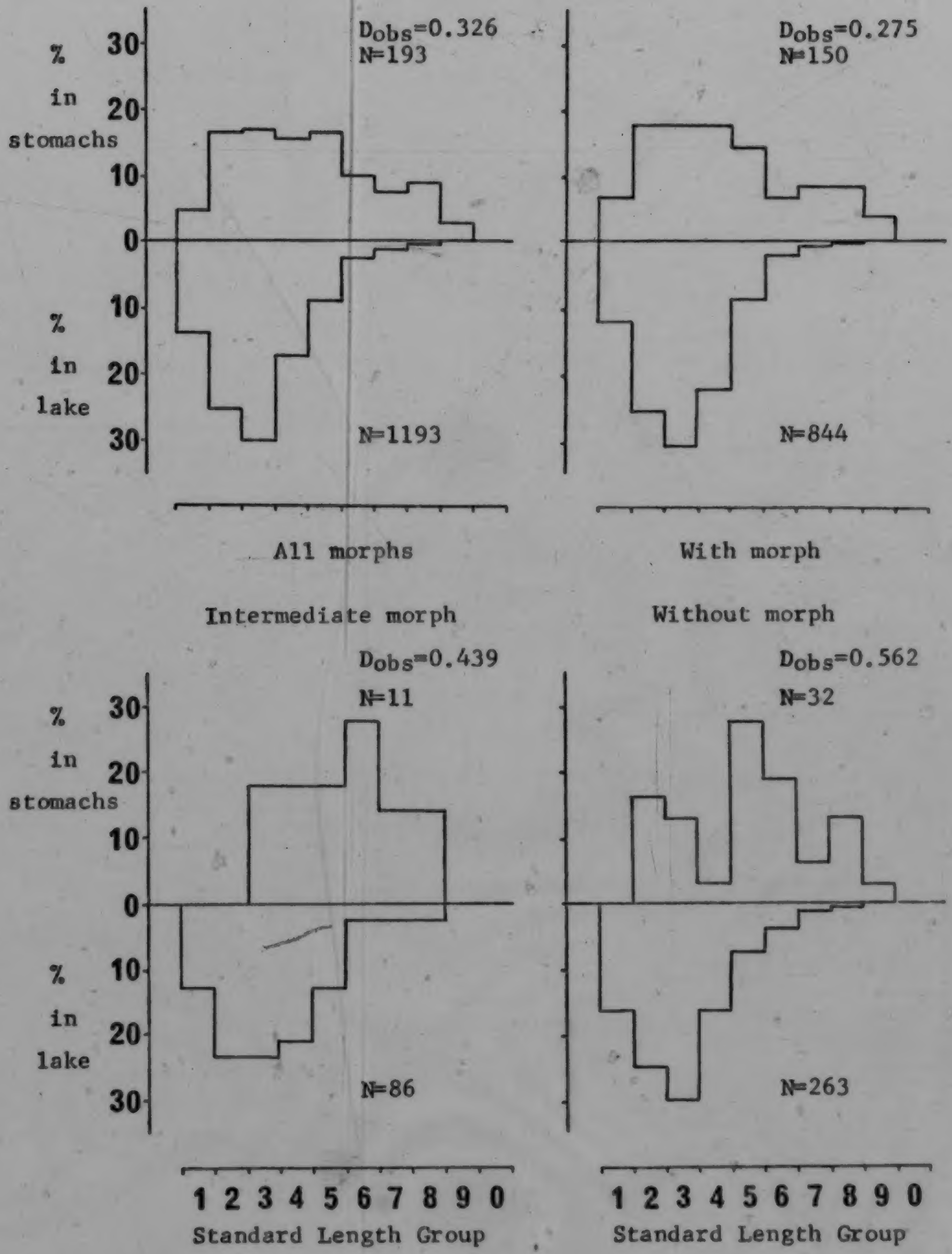
$X^2 = 0.919$ ($p \cong 0.5$)

Table 27: Dorsal spine frequencies in pike stomachs compared to frequencies in the lake.

Year	# of Dorsals	Frequency In Lake (%)	Frequency In Stomach (%)	Electivity Index
1976	4	10 (2.1)	1 (1.5)	-0.167
	5	344 (72.1)	50 (74.6)	+0.017
	6	122 (25.6)	16 (23.9)	-0.034
	Total	477	67	
	$X^2 = 0.25$ ($p \cong 0.9$)			
1977	4	10 (2.9)	0 (0.0)	-1.000
	5	219 (64.2)	34 (68.0)	+0.029
	6	112 (32.8)	16 (32.0)	-0.012
	Total	341	50	
	$X^2 = 1.59$ ($p \cong 0.5$)			
Both	4	20 (2.4)	1 (0.8)	-0.500
	5	563 (68.8)	84 (71.8)	+0.021
	6	234 (28.6)	32 (27.4)	-0.021
	Total	818	117	
	$X^2 = 1.41$ ($p \cong 0.5$)			

Figure 5: Standard length distribution of prey and lake sticklebacks. Relative frequency of 1976 and 1977 samples combined, $D_{0.01} = 0.161$, identified and unidentified morphs combined.

Standard Length Group	Standard Length Range (mm)
1	15-19.9
2	20-24.9
3	25-29.9
4	30-34.9
5	35-39.9
6	40-44.9
7	45-49.9
8	50-54.9
9	55-59.9
0	60+


Dobs=0.326
N=193
N=1193
All morphs
Dobs=0.275
N=150
N=844
With morph
Intermediate morph
Dobs=0.439
N=11
N=86
Without morph
Dobs=0.562
N=32
N=263
% in stomachs
% in lake
30
20
10
0
10
20
30
1 2 3 4 5 6 7 8 9 0
Standard Length Group

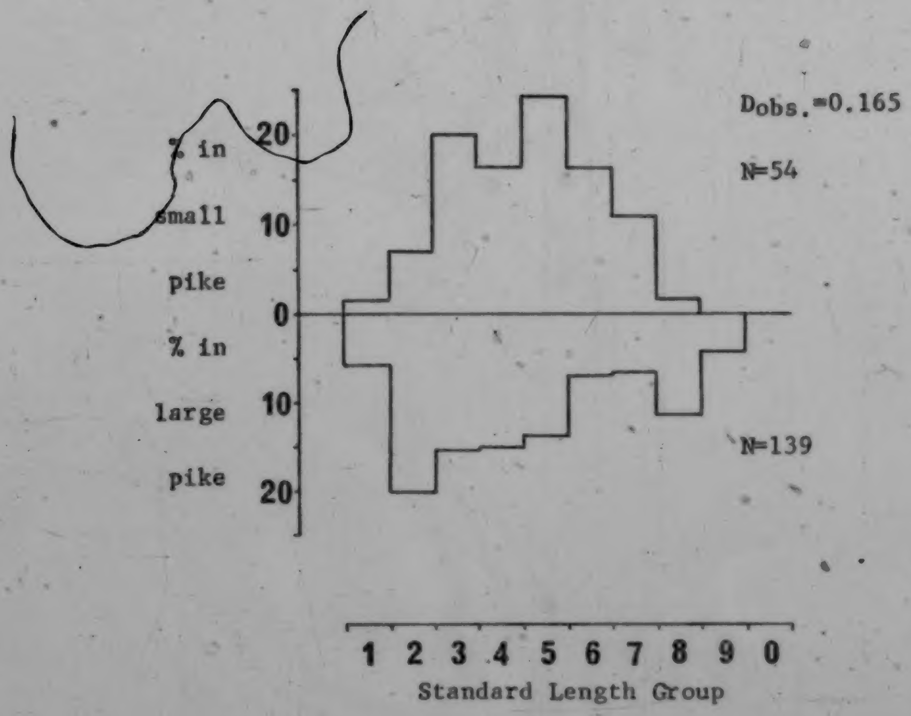


Figure 6: Distribution of prey items in small and large pike predators. 1976 and 1977 identified and unidentified morphs combined. Abbreviations and standard length groups are defined in Figure 5.

minnows during the sampling periods. The much lower percentage for 1977 is partially due to increased representation of invertebrate prey items (21.2%) and fatheads (9.4%) in small pike (only two small pike were taken in 1976, both contained stickleback prey only). Large pike prey little on invertebrates (0.4%) and fatheads (0%). Large pike are more liable to be empty (50%) than small pike (14.7%) but large pike contain on average more prey fish (88 fish/13 pike = 6.8) than small pike (243 fish/81 pike = 3.0), (1977 data only). Pike which had fish in their guts averaged 8.2 and 2.4 Culaea prey items per pike, respectively for 1976 and 1977. This times a conservative summer digestion rate of two days (J. Diana, pers. comm.) indicates that over the summer study period (June-September) each pike in Wakomao Lake would eat a minimum of 5.3 x $\frac{120}{2}$ = 318 sticklebacks. This figure times 161 pike collected gives a minimum stickleback consumption of 51,200 for just the summer period for the pike collected. These figures represent minimal estimates since unidentified prey fish nor fragments of prey fish were not counted.

Discussion

From the crude estimates made above and considering that pike density in Wakomao Lake is relatively high (no diminishing gill-net returns were noted), it is clear that pike maintain considerable predation pressure upon the Wakomao Lake stickleback population.

Ivlev (1961) has pointed out that selection of prey items depends upon two major factors: preference of the predator and accessibility of the prey. These in turn may be subdivided further into several components. Preference is determined by physiological properties such as degree of satiation, innate inclination and past experience (learning or conditioning) and is strictly a predator phenomenon. Accessibility includes aspects of the biology of both the predator and the prey such as their relative abundance, size, spatial distribution and predatory or defensive behaviour (Ivlev, 1961). Any single predatory situation involves all these parameters thus the outcome is likely to vary with any alteration of these factors.

The pike's preference for either pelvic morph is the same when the predator is larger than about five times the stickleback's size, that is, no change in morph selectivity was noted over the size range of pike collected (18-64 cm SL). Thus, the factor accounting for the differential morph representation in the pike stomachs must be due to differential accessibility of the pelvic morphs, most likely due to the behavioural differences shown previously.

The attempts by pike to select as large a prey item as possible are expected since the optimal prey size (1/2 to 1/3 the length of the predator), (Scott and Crossman, 1973) is far greater than the maximum size of the sticklebacks. Ivlev (1961) has experimentally shown that pike prefer the largest prey items it is possible for them to ingest. This would also be expected from an energetics point of view. Such size selection would create a selective pressure favouring reproduction at smaller size (or earlier ages). A similar situation exists in Gasterosteus aculeatus (McPhail, 1977) in which predation by trout has been implicated as a mechanism for selection of extremes in breeding sizes. Moodie (1977) has noted that the maximum body size of Culaea tends to be smaller in populations subject to potential predation by Esox and Perca and salmonids. Predator selection for large individuals as noted here could be the causative agent for these results. Indirectly, size selective predation forcing earlier reproduction might have an effect upon pelvic development. That is, early reproduction would put a premature energy demand upon the sticklebacks and the non-development of minimally useful structures would allow this energy to be put into reproductive effort. Without females from Astotin Lake average slightly more eggs than do withs (Nelson and Atton, 1971). Kaminski (1977ms) implies that females without spines initiate ovarian development earlier than those with spines since they can devote more energy to ovarian development and maintenance.

The selection for large withs indicates that predation by pike is not the selective force responsible for the decline in without frequency with age and overwinter, as noted earlier. The without morphs (especially large ones) seem to be less accessible to the pike in Wakomao Lake probably due to the better developed behavioural defences noted earlier.

The lack of selection of either dorsal spine category is contrary to the expectations from the laboratory predation experiments. Differential modification of defensive behaviour of five and six dorsal spined fish, due to the laboratory situation may be the cause for this.

Predation by pike upon the sticklebacks in Wakomao Lake is influenced by several factors, most notably prey morph and associated behavioural differences which determine morph accessibility, and prey size with its associated difference in the degree of defensive behavioural development. With respect to wild pike predators, with morphs (especially large ones) are at a disadvantage relative to without morphs, thus predisposing them to greater potential (or actual) predation by northern pike.

GENERAL DISCUSSION

Synthesis of Results

The results from the various aspects of this study may be synthesized into a coherent picture of anti-predator adaptation in the Wakomao Lake population of Culaea inconstans. However, it should be remembered that the predators considered in this study are opportunists; so their diet in the lake is not restricted to sticklebacks. Except in the case of pike, the actual influence of the predators upon Culaea is difficult to gauge. Field work is needed to demonstrate the influence of these predators on the lake population to permit generalizations to be made from the laboratory experiments.

Pike exert a significant and probably continuous influence upon the sticklebacks, consuming more of them than the alternate minnow prey also found in the lake. The pelvic morphs are not differentially distributed in the lake thus are equally available to the pike, at least on a gross level. On a morphological basis, withouts are preferred, especially by small pike but they are less accessible due to better developed defensive behaviour. The between morph behavioural differences identified in the laboratory studies probably contribute to the selective predation observed in wild pike.

A similar situation exists in predatory situations involving dytiscid larvae - the withs are more accessible due to a behavioural difference, consequently they are selectively preyed upon (at least in the lab). Dytiscid larvae which occur at relatively high densities at certain times of the year have a potentially great predatory influence on the *Culaea* population.

No selective predation by *Lethocerus* was demonstrated thus suggesting that predation by this bug on the pelvic morphs is a chance event related to the frequencies of the morphs in the prey population. This implies no selective predation would occur in the lake situation (but see ~~the~~ frequency dependent discussion below). Due to low densities in Wakomao Lake the impact of *Lethocerus* predation upon the *Culaea* population is probably low.

Other predators such as dragonfly nymphs and possibly birds may preferentially prey on the without morphs for behavioural or morphological reasons thus creating a counter selective force. Piscivorous birds and dragonfly nymphs of various species occur in large numbers at Wakomao Lake but their influence on the *Culaea* population is not known. Unknown agents seem to selectively remove without and intermediate morphs over the winter but more work is required to elucidate their nature and influence.

The anti-predator adaptations of *Culaea inconstans* in Wakomao Lake are a compromise between all aspects of the selective regime. Selection of one morph or the other in the lake situation may be expected to be complicated by factors such as size (age) of stickleback, presence and amount of cover vegetation, satiation of the predator, predator/prey size ratio (especially in pike), past experience of the prey and the type of predator. In some situations selection is on with morphs, in others it is on the without morphs. Other features of the stickleback's environment, not investigated here, such as other predators and other functions of the pelvic spines, e.g. intraspecific agonism (McKenzie, 1969a) or mating (McKenzie, 1969b) will exert different selective pressures upon the presence or absence of the spines.

In view of the uniqueness of each predatory situation and the many selective pressures possible it is perhaps misleading (but intuitively pleasing and experimentally simple) to search for 'the' biological function of a single morphological or behavioural difference (Liley and Seghers, 1975). In the current case from the available evidence, it seems that predation exerts a large if not significant influence upon the pelvic polymorphism.

Discussion

The observed frequency of pelvic morphs at any site or point in time may be due to a variety of causes (assuming as noted previously that the sampling was random, no differential dispersal of morphs occurs, differential reproduction or mating does not occur and all scoring of morphs was accurate).

Linkage of the pelvic locus with other loci could result in a polymorphic equilibrium situation maintained by the adaptiveness (or lack thereof) of the other loci. Pleiotropic effects of other loci upon the pelvic locus may influence the expression of pelvic genotype, thus varying the phenotypic frequency. Both of these agents probably influence the pelvic polymorphism to some degree but it is impossible at present to gauge their effect.

There is a possibility that the pelvic polymorphism may simply be due to neutral variation and the observed frequencies would result from a Hardy-Weinberg equilibrium probably involving linkage or pleiotropy. Regal (1977) has argued that the shutting off of messages controlling processes or structures not vital to survival would be preferred, since it would decrease the 'noise' hence ambiguity in the information transfer system (i.e. from DNA to structure). However, from the accumulated evidence selective neutrality of the pelvic apparatus is unlikely.

Random genetic drift seems unlikely in the present case due to the very large population size, probably much greater than one million individuals.

Differential directional selection of the pelvic morphs is the final cause by which such a polymorphism might occur. The accumulated evidence tends to support such selection. These selective forces may be either abiotic or biotic in origin. Abiotic forces which may affect the pelvic polymorphism in Culaea were not investigated in this study, hence their influence is unknown.

There are several mechanisms by which a stable polymorphism may be maintained by selective pressures. Heterozygote superiority (heterosis) such as seen in sickle cell anemia (Ford, 1975) is unlikely in Culaea since the intermediates (morphological) occur in low frequencies and there is some evidence for selection against them.

Endocyclic selection (Ford, 1975) in which one morph is more fit at one time in ontogeny and the other morph fitter later may result in a stable polymorphism, but this, at present is untested in this population. Differential selection of this type could operate before the morphs are scoreable thus biasing the morph frequency distribution upon which subsequent selection operates. McPhail (1969) has noted this situation in Gasterosteus aculeatus in which the frequency of adult phenotypes of 'Black' and 'Red' are established by predator selection responding to behavioural differences in phenotypically unscoreable young.

Cyclical selection (Ford, 1975) with one morph enjoying a relative advantage during one season and the other during another season is also a possibility. Given the extreme seasonality of the Wakomao Lake environment it is likely that the optimum phenotype shifts according to season in response to the selective pressures operating at that time. This in itself would maintain a polymorphism. Some evidence exists that supports such seasonal selection in Wakomao Lake, specifically, the seasonal variation in without frequency. This study only considered selection operating at one point (summer) of the yearly life cycle of the stickleback; thus there is an inherent bias when interpreting the results.

Frequency-dependent mechanisms in which an inverse relationship exists between genotypic frequency and fitness can theoretically maintain stable polymorphisms (Ayala and Campbell, 1974; Maynard Smith, 1970). Predation may have an effect either in a mimicry situation, unlikely here since there is no distasteful model, or, as Clarke (1962) has shown, the formation by a vertebrate predator of a search image for a common morph might favour a rare morph even if it was more conspicuous. This apostatic selection (Clarke, 1962) possibly may maintain the pelvic polymorphism, but it is unlikely since the morphological search image for withs and withouts must be very similar. Stereotyped defensive behaviour (such as spine erection) which may be learned and evolutionarily capitalized upon by a predator may be expected to result in a selective disadvantage relative to protean (erratic) defensive flight (Humphries and Driver, 1970). Sufficient behavioural stereotypy in the commonest morph could result in a behavioural search image being developed for that morph. This would satisfy the requirements of apostatic, frequency dependent selection. However, selective predation due to this is probably obscured by the actual selective value of the differences themselves, that is, the selection noted is due to differences in morph accessability and not to differences in the search image of the predator. Humphries and Driver (1970) also argue that the use of defensive behaviours unfamiliar to the predator, since they are selectively favoured,would lead to an increase in intraspecific diversity of escape behaviours. The corollary of this is much individual variation in behaviour when confronted with a predator - a situation amply evident in this study.

Maynard Smith (1970) notes that biochemical variants may differ in their susceptibility to parasites or disease. Selection on both homozygotes alternating between generations could result in cyclical changes in gene frequency (Maynard Smith, 1970). Both these latter possibilities require special conditions improbable in the present situation.

The frequency dependent mechanisms noted by most authors rely upon the predator being the active selective agent; the prey is passively polymorphic. Given an ambush predator such as Lethocerus which consumes only prey coming to it (i.e. the predator is passive); then the probability of capture of an individual of each morph is equal, given no other between morph differences. Thus, predation upon the morphs may be expected to be in proportion to the frequency of those morphs in Wakomao Lake. However, if an inverse relationship between morph frequency and fitness with respect to Lethocerus could be demonstrated, then maintenance of the withouts at low frequencies could occur. Such a relationship could come about by density-dependent differences between the morphs, e.g. different structuring of schools at different frequencies of morphs etc. The effect of this upon the Wakomao Lake polymorphism is probably low due to the low density of these bugs but rigorous testing of this hypothesis may yield information applicable to other situations with different morph frequencies.

A final frequency-dependent mechanism noted by Maynard Smith (1970) relies upon different genotypes having different fitnesses in the available ecological niches. This diversifying natural selection (Dobzhansky et al., 1977) seems the most likely mechanism maintaining the pelvic polymorphism in Wakomao Lake.

Ecological division of the environment by the morphs is not evident. Rather, the necessary range of subenvironments required by diversifying natural selection is due to the types of predators and their respective methods of predation. With respect to these predators, two adaptive subniches exist. The withouts are more fit with respect to pike and dytiscid predators. The withs are more fit during predation by Aeschna (and during winter, for unknown reasons; perhaps predation when little cover vegetation is present), and possibly early in ontogeny due to size influences of the erectile spines upon predators. Evidence supporting the advantages of the with morphs is weak in this study; but withs must have an advantage, either during predation or from other selective pressures, or else they would not be observed in the frequency which occurs in the lake. This may be due to a morphological advantage or to associated behavioural advantages. Continuous gene flow of morphs from another area or differential gene flow (of with genes) could also be factors maintaining high with frequencies. Predation by piscivorous birds influences the morph frequencies to an unknown degree. The maximum size of the bird's bill (depth or width) would not greatly exceed the size (TBD) of the commonly captured prey. Since sticklebacks can increase their total body depth at will, it is reasonable to expect that morphs possessing pelvic spines would be at a morphological advantage relative to withouts during bird predation.

The relative fitness of the morph is determined by its morphology, that is, pelvic condition, as well as by its behaviour when confronted with a predator. Both these characters act in concert or in opposition to affect the outcome of predation events.

Behaviour is perhaps the most labile, hence the most responsive trait to evolutionary pressures. Similar work on Gasterosteus aculeatus has resulted in discovery of behavioural differences associated with a morphological difference (Larson, 1976; T. E. Reimchen, pers. comm.) which reinforced separation between the morphs. The differential responses of sticklebacks from different areas to the same predator confirms that behaviour plays an important anti-predation role in some populations of Culaea.

The differential responses of predators (pike) from two different areas suggests that past experience (both evolutionarily and within an individual's lifetime) with the prey item influences the predatory act. That is, not all predators are equivalent in their response to prey items. The coevolution of a predator-prey relationship or the 'arms race' between predator and prey (Edmunds, 1974) results in both groups being adequately adapted to the situation in which they occur. In view of this, it is perhaps unrealistic to expect highly significant results in laboratory experiments involving such co-adapted entities. That such differential results occur may indicate more the disturbance or lack of reproduction of the natural environment than better or less adapted defensive mechanisms.

The low frequency intermediate morphs, not considered in the experimentation, are predicted on the basis of the above conclusion to occupy a less adaptive area (most likely behavioural) between the subniches of the withs and withouts.

Thus, the pelvic polymorphism in Wakomao Lake is maintained at least partially by predation pressure. This conclusion agrees well with Nelson's (1969) original hypothesis that local variation in the selective environment and lack of alternate prey force piscivorous predators from central Alberta and Saskatchewan to consume sticklebacks. This favours escape responses such as streamlining the body which in its extreme leads to pelvic loss and the polymorphism. From this conclusion it may be expected that situations with radically different frequencies of pelvic phenotypes will also differ in the number and types of predators, both invertebrate and vertebrate, present. This may be the situation causing the slight geographic variation of pelvic morph frequency seen in the Redwater system. In Whitemud Creek, another river system of the Edmonton area, the morph frequency varies dramatically from the confluence with the North Saskatchewan River to the headwaters. The environmental situation (and presumably the predators) also varies considerably.

Nelson (1977, p. 1319) notes that the loss of the pelvic skeleton might result from either "relaxation of selective pressures favouring its full development or to selective pressures favouring loss." He further states that the former explanation seems probable in localities exhibiting much variation in expression of the pelvic condition while the latter is applicable to areas in which withouts predominate. The present results disagree, in that, in this lake with considerable variation of expression there exist many selective pressures favouring either loss of the pelvic girdle or expression of pleiotropically associated defensive behaviours. Thus, it would seem that rather than relaxation a shifting of selective pressures (evolutionarily and geographically) has caused the polymorphism.

Nelson (1977) also points out that if, in addition to the adaptive peaks noted here for the extreme types, assortative mating occurs and if selective pressures exist against the intermediates, then the situation with Culaea may well be the precursor to that noted by Larson (1976) in which spatial and dietary differences, as well as morphological and behavioural differences exist between benthic and limnetic forms of Gasterosteus aculeatus. Both of these situations are the theoretical, initial stages of the sympatric speciation model (Endler, 1977; Mayr, 1963; Ross, 1974) by diversifying natural selection.

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APPENDIX 1

The Stickleback Collections at Each Site

Table 28: Wakomao Lake collections. Site location: 54°09' N 113°32' W. (Note in tables following * = sample with unscoreable fish not included.)

Collection Number	Date			Pelvic Morph Frequency				
	Day	Month	Year	with	intermediate spined	intermediate spineless	without	N
Dipnet, bagseine and electrofisher collections								
76-3	04	vi	1976	171	13	15	50	249
76-4	18	vi	1976	324	26	16	111	477
77-2-a	12	v	1977	145	2	5	36	188
77-4	01	vi	1977					142 *
77-6-b 1/2 young	08	vi	1977	53	1	4	10	68 *
adult				10	0	2	1	13
77-9-b	20	vi	1977	108	5	3	46	162 *
77-10-a	28	vi	1977	92	7	3	23	125
77-10-b 1/3	28	vi	1977	83	6	2	32	123
2/3	28	vi	1977	84	3	4	32	123
3/3	28	vi	1977	83	0	0	18	101
77-11-a	07	vii	1977	214	12	4	71	301
77-12-b	13	vii	1977	163	6	1	35	205
77-14-a	20	vii	1977	251	9	8	71	339 *
77-14-b	20	vii	1977	152	6	8	57	223
77-14-c	20	vii	1977	160	5	7	42	214
77-14-j	21	vii	1977	73	3	1	20	97
77-16	28	vii	1977	72	0	6	23	101
77-19-d	10	viii	1977	40	4	1	16	61
77-19-e	10	viii	1977	62	3	1	23	89

Collection Number	Date			Pelvic Morph Frequency				
	Day	Month	Year	with	intermediate		without	N
					spined	spineless		
77-19-f	10	viii	1977	72	3	0	24	99
77-19-g	10	viii	1977	60	2	0	17	79
77-19-i	11	viii	1977	88	6	3	32	129
77-20-f	18	viii	1977	110	5	7	26	148
77-21-j	25	viii	1977	71	3	6	29	109
77-21-k	25	viii	1977	26	3	2	11	42
77-21-l	25	viii	1977	85	7	3	29	124
77-21-m	26	viii	1977	89	1	4	33	127
77-21-n	26	viii	1977	240	11	0	95	346
77-21-o	26	viii	1977	145	5	1	55	206
77-22-b	08	ix	1977	182	7	12	60	259
77-24-a	20	ix	1977	154	6	5	50	215
77-26-b	11	x	1977	142	10	2	46	200
77-27-a-c	25	x	1977	211	8	8	59	286
Minnow trap collections								
77-6-b 2/2	08	vi	1977	5	0	1	2	7
77-14-d	20	vii	1977	21	0	2	8	31
77-14-f	20	vii	1977	24	1	3	3	31
77-14-i	21	vii	1977	7	0	0	4	11
77-19-c	10	viii	1977	1	0	0	2	3
77-20-c	17	viii	1977	4	0	0	3	7
77-20-e	18	viii	1977	4	1	1	1	7
77-20-h	19	viii	1977	4	0	0	1	5

Table 29: Wakomao Creek collections.

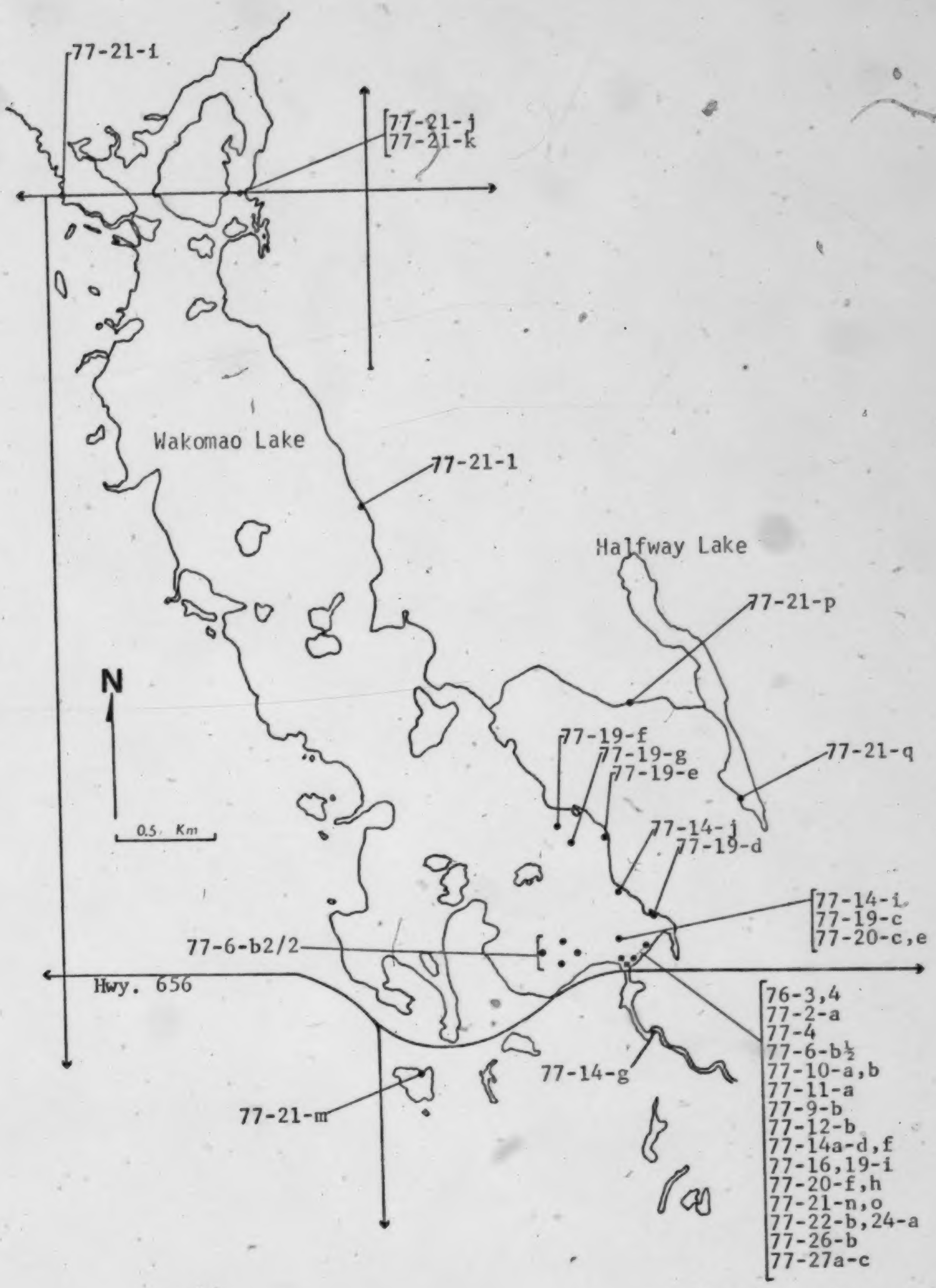
Collection Number	Date			Pelvic Morph Frequency				
	Day	Month	Year	with	intermediate		without	N
					spined	spineless		
Site: $54^{\circ}08'$ N $113^{\circ}31'$ W - Outlet Creek (south of Wakomao Lake)								
77-14-g	20	vii	1977	190	9	8	64	271 *
Site: $54^{\circ}11'$ N $113^{\circ}34'$ W - Wakomao Creek (north of Wakomao Lake)								
77-21-i	25	viii	1977	79	2	2	34	117
Site: $54^{\circ}13'$ N $113^{\circ}36'$ W - Wakomao Creek (north of Wakomao Lake)								
77-2-b	12	v	1977	97	0	6	28	131
77-13-b	19	vii	1977	160	6	2	57	225
77-21-c	23	viii	1977	65	3	2	21	91
Site: $54^{\circ}13'$ N $113^{\circ}31'$ W - Wakomao Creek (north of Wakomao Lake)								
77-2-c	12	v	1977	45	1	4	12	62
77-13-c	19	vii	1977	118	0	1	36	155 *
77-21-d	23	viii	1977	84	0	1	35	120

Table 30: Collections from other areas in the Redwater System.

Collection Number	Date			Pelvic Morph Frequency				
				with	intermediate		without	
	Day	Month	Year		spined	spineless		N
Site: $54^{\circ}04'$ N $113^{\circ}19'$ W - Redwater River								
UAMZ 3852	04	vi	1977	73	1	2	25	101
Site: $54^{\circ}03'$ N $113^{\circ}40'$ W - Redwater River								
77-13-a	19	vii	1977	12	1	0	6	19
Site: $54^{\circ}06'$ N $113^{\circ}28'$ W - Redwater River								
77-2-k	13	v	1977	76	2	3	28	109
77-2-1	13	v	1977	72	3	6	21	102
77-9-a	20	vi	1977	160	5	3	62	230
77-12-a	13	vii	1977	10	1	0	3	14
77-21-b	22	viii	1977	94	6	6	29	132 *
Site: $54^{\circ}05'$ N $113^{\circ}24'$ W - Redwater River								
77-2-p	13	v	1977	13	0	0	2	13
Site: $54^{\circ}04'$ N $113^{\circ}28'$ W - Fairydell Creek								
76-2	04	vi	1976	152	5	6	51	214
77-2-s	13	v	1977	11	0	0	6	17
77-21-a	22	viii	1977	72	4	6	23	105
Site: $54^{\circ}04'$ N $113^{\circ}18'$ W - creek outflow from Halfmoon Lake								
77-2-q	13	v	1977	93	4	4	31	132

Collection Number	Date			Pelvic Morph Frequency				
	Day	Month	Year	with	intermediate spined	intermediate spineless	without	N
Site: 54°06' N 113°27' W - unnamed lake, beaver pond east of Redwater River								
77-2-m	13	v	1977	51	1	1	11	64
77-2-o	13	v	1977	617	13	21	155	806
Site: 54°09' N 113°31' W - Halfway Lake								
77-21-q	27	viii	1977	71	1	1	39	112
Site: 54°09' N 113°32' W - ditch between Halfway Lake and Wakomao Lake								
77-21-p	27	viii	1977	105	4	3	33	145
Site: 54°11' N 113°28' W - West Bridges Lake								
77-1-c	07	v	1977	92	1	4	22	120
77-6-c	09	vi	1977					324 *
77-13-f	19	vii	1977	62	1	0	31	95
77-21-g	23	viii	1977	51	2	0	22	75
Site: 54°11' N 113°27' W - creek between Bridges' Lakes								
77-2-d	12	v	1977	14	0	3	2	19
77-13-e	19	vii	1977	127	5	3	38	173
77-21-f	23	viii	1977	78	4	4	24	110
Site: 54°13' N 113°27' W - creek south of Duggans Lake								
77-13-d	19	vii	1977	143	7	5	42	197
77-21-e	23	viii	1977	83	4	2	19	108

Figure 7: Wakomao Lake and Halfway Lake. ● = *Culaea* collection sites, ■ = *Esox* collection sites. From aerial photos taken in 1973. Hwy. = Highway; secondary roads are also shown.


77-21-i
77-21-j
77-21-k
Wakomao Lake
77-21-1
Halfway Lake
77-21-p
N
77-19-f
77-19-g
77-19-e
77-21-q
0.5 Km
77-14-j
77-19-d
77-14-i
77-19-c
77-20-c,e
77-6-b2/2
Hwy. 656
76-3,4
77-2-a
77-4
77-6-b½
77-10-a,b
77-11-a
77-9-b
77-12-b
77-14a-d,f
77-16,19-i
77-20-f,h
77-21-n,o
77-22-b,24-a
77-26-b
77-27a-c
77-14-g
77-21-m

APPENDIX 2

Possible Biases of the Collection Methods

When a large polymorphic population of mobile organisms is being investigated it is pertinent to know whether any collecting method differentially selects for one of the morphs. To investigate this a series of comparison collections were made on a 5 meter by 10 meter quadrat on the sand beach area of Wakomao Lake. The water depth in the quadrat ranged from 0.2 to 1.0 m, vegetation was sparse with grasses or Cladophora sp. present. The area was sequentially collected on 20 July 1977 by bagseine, dipnet and electroshocker.

Collection #	Method	Frequency of Pelvic Morphs			N
		with	intermediate	without	
77-14-a	bagseine	251	17	71	339
77-14-b	dipnet	152	14	57	223
77-14-c	electrofisher	160	12	42	214
	Total	563	43	170	776
	Percent	72.5	5.5	21.9	

$X^2 = 2.84$ ($p \cong 0.8$)

Collection #	Method	Dorsal Spine Number			N
		4	5	6	
77-14-a	bagseine	10	219	112	341
77-14-b	dipnet	3	149	71	223
77-14-c	electrofisher	11	137	66	214
	Total	24	505	249	778
	Percent	3.1	64.9	32.0	

$X^2 = 5.49$ ($p \cong 0.4$)

Differential collection of either pelvic morphs or fish with different dorsal spine counts did not occur.

A fourth collection method was baited minnow traps, usually set near the lake bottom in the southeast portion of Wakomao Lake. Collections by this method are:

		Frequency of Pelvic Morphs			
Collection #	Method	with	intermediate	without	N
77-14-c	Total	563	43	170	776
	Minnow Traps	70	9	24	103

$\chi^2 = 2.02$ ($p \cong 0.4$)

		Dorsal Spine Number			
Collection #	Method	4	5	6	N
77-14-c	Total	24	505	249	778
	Minnow Traps	2	60	41	103

$\chi^2 = 2.72$ ($p \cong 0.35$)

No bias for pelvic morph or dorsal spine number occurs in the minnow trap collections when compared to other collection methods.

APPENDIX 3

Ecology of Wakomao Lake Sticklebacks

Table 31: Vegetation of Habitats defined in Wakomao Lake.

#	Habitat Name	Depth Range (m)	Major Vegetation Species	% Coverage of Substrate
1	Burreed - Typha shoreline	0.0-1.0	Sparganium chlorocarpum	25-75
			Typha latifolia	25-50
			Filamentous algae	25
2	Scirpus shoreline	0.0-1.5	Scirpus validus	50
			S. microcarpus	10
			Carex sp.	5
3	Myriophyllum-Lemna floating on shore	0.0-0.5	Myriophyllum sp.	70+
			Ceratophyllum sp.	5
			Lemna trisculca	0-25+
4	Myriophyllum, rooted submerged on shore	0.0-1.0	Myriophyllum sp.	30-50
			Ceratophyllum sp.	5
			Filamentous algae	25
5	Sand beach	0.0-1.5	Carex sp.	0-2
			Debris	0-2
6	Submerged Cladophora mats on sand beach	0.5-1.5	Cladophora sp. plus other filamentous algae	90-100
			Lemna sp.	5
			Other	5
7	Offshore Myriophyllum-Potamogeton	2+	Myriophyllum sp.	30-90+
			Ceratophyllum sp.	5
			Lemna sp.	
			Potamogeton richardsonii	0-80+
			P. pectinatus	10-20

Table 32: Individual collections of pelvic morphs from each habitat in Wakomao Lake.

Habitat #	Collection #	Morph Frequency				N
		with	intermediate		without	
			spined	spineless		
1	77-21-j	71	3	6	29	109
	77-19-d	40	4	1	16	61
			$X^2 = 2.81\ (p \cong 0.6)$			
2	77-20-f	109	4	3	31	147
	77-19-i	87	6	4	33	130
	77-14-j	73	3	1	20	97
	77-12-b	163	6	1	35	205
			$X^2 = 9.18\ (p \cong 0.6)$			
3	77-21-l	85	7	3	29	124
	77-21-n	240	11	0	95	346
			$X^2 = 10.4\ (p < 0.05)$			
		due to lack of intermediates - sampling bias.				
4	77-19-e	62	3	1	23	89
	77-21-o	145	5	1	55	206
			$X^2 = 0.58\ (p = 0.9)$			
5	77-10-b (2/3)	84	3	4	32	123
	77-14-b	152	7	4	60	223
			$X^2 = 0.9\ (p \cong 0.7)$			
6	77-10-b (1/3)	83	6	2	32	123
7	77-19-f	72	3	0	24	99
	77-19-g	60	2	0	17	79
			$X^2 = 0.24\ (p \cong 1.0)$			

Table 33: Dorsal spine - pelvic morph association for each sample.

	Dorsal Spine Number				
Pelvic Morph	4	5	6	7	N
Collection #: 76-4, 1976					
with	8	225	90	1	324
intermediate	1	34	7	0	42
without	1	85	25	0	111
		$X^2 = 7.15$ ($p \cong 0.4$)			
Collection #: 77-14-a, 1977					
with	7	159	85	0	251
intermediate	0	9	8	0	17
without	3	49	19	0	71
Collection #: 77-14-b					
with	1	102	50	0	153
intermediate	0	11	3	0	14
without	2	36	18	0	56
Collection #: 77-14-c					
with	5	104	51	0	160
intermediate	1	7	4	0	12
without	5	26	11	0	42
Total 1977					
with	13	365	186	0	564
intermediate	1	27	15	0	43
without	10	111	48	0	169
		$X^2 = 6.61$ ($p \cong 0.2$)			

Predators of Wakomao Lake

The following potential predators of *Culaea inconstans* were found in Wakomao Lake in 1977:

Pisces
- *Esox lucius* Linnaeus - Northern Pike

Aves
- *Gavia immer* (Brunnich) - Common Loon
- *Podiceps grisegena* (Boddaert) - Red-Necked Grebe
- *Podiceps auritus* (Linnaeus) - Horned Grebe
- *Podilymbus podiceps* (Linnaeus) - Pied-Billed Grebe
- *Ardea herodias* Linnaeus - Great Blue Heron
- *Botaurus lentiginosus* (Rackett) - American Bittern
- Laridae - Gulls, Terns, etc.
- *Megaceryle alcyon* (Linnaeus) - Belted Kingfisher

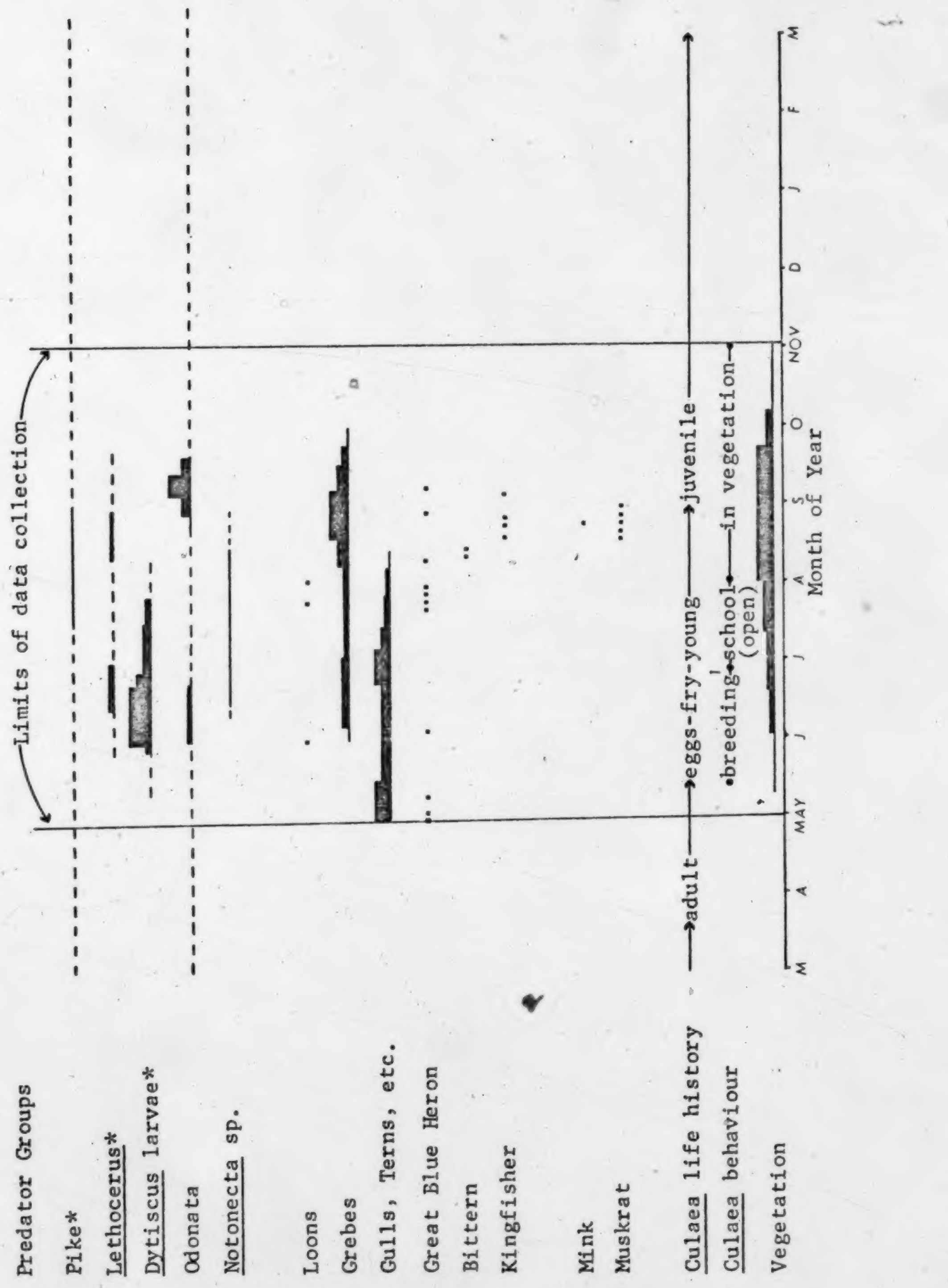
Mammalia
- *Mustela vison* Schreber - American Mink
- *Ondatra zibethicus* (Linnaeus) - Muskrat

Insecta
- Odonata - Dragonflies (*Aeschna* sp. and *Anax* sp.?)
- *Lethocerus americanus* (Leidy)
- *Notonecta* sp.
- *Dytiscus* sp.

Their approximate abundance is shown in Figure 8.

Figure 8: Occurrence of potential predators of _Culaea inconstans_ at Wakomao Lake (1977). Width of line indicates approximate relative abundance within the group. ---- = hypothesized presence of predator. • = single sighting. * = predators dealt with in this study.

1. _Culaea_ adults may prey upon conspecifics eggs or larvae (Wootton, 1976, K. Hirai pers. comm.).


Predator Groups
Pike*
Lethocerus*
Dytiscus larvae*
Odonata
Notonecta sp.
Loons
Grebes
Gulls, Terns, etc.
Great Blue Heron
Bittern
Kingfisher
Mink
Muskrat
Culaea life history
Culaea behaviour
Vegetation
Limits of data collection
adult
eggs-fry-young
juvenile
breeding
school
(open)
in vegetation
M
A
MAY
J
J
A
S
O
NOV
D
J
F
M
Month of Year

APPENDIX 4

Results of Individual Predation Experiments

Hypergeometric chi-squares are noted; superscripts are * $p < 0.05$, ** $p < 0.025$, *** $p < 0.01$; subscript is 1 = Yates' correction for continuity applied.

Table 34: 1976 morph consumption by northern pike.

Experiment Number	Prey Mean SL(mm)	With Morph # Offer	With Morph # Ate	Without Morph # Offer	Without Morph # Ate	Hyper. X^2
Wakomao Lake fish: (Mixed dorsal counts)						
a) Medium prey fish						
B5	34.7	15	4	13	6	
B8	32.0	15	4	15	9	
Subtotal		30	8	28	15	4.31 *
b) Large prey fish:						
B6	42.9	14	4	15	9	
B9	45.0	15	6	15	7	
B14	43.4	10	5	8	5	
Subtotal		39	15	38	21	2.15
Total (5 replicates)		69	23	66	36	6.12 **
Fairydell Creek fish: (Mixed dorsal counts, mixed sizes)						
B1	?	24	7	23	14	4.67 *
Whitemud Creek fish: (Mixed dorsal counts)						
B11	54.4	14	6	15	9	
B12	42.6	15	8	15	7	
B13	49.2	8	5	9	5	
B15	57.7	10	4	10	5	
Total (4 replicates)		47	23	49	26	0.16

Table 35: Consumption of unaltered pelvic morphs by northern pike.

Experiment Number	Prey Mean SL(mm)	With Morph # Offer	With Morph # Ate	Without Morph # Offer	Without Morph # Ate	Hyper. X^2
Cover vegetation present:						
a) Small prey fish						
5 dorsal spines						
1b	24.6	15	10	15	11	
4b	24.3	15	4	15	6	
5b	23.9	15	4	15	7	
4c	28.2	14	4	15	8	
5c	27.5	15	8	15	7	
Subtotal		74	30	75	39	1.95
6 dorsal spines						
2b	23.7	15	7	15	6	
3c	22.6	15	7	15	6	
Subtotal		30	14	30	12	0.27
X^2 between dorsal variants		0.13		0.44		
Total (7 replicates)		104	44	105	51	0.82
b) Medium prey fish						
5 dorsal spines						
1c	31.5	14	13	13	7	
4e	34.3	13	7	15	7	
4g	36.8	15	7	15	7	
Subtotal		42	26	43	21	1.45
6 dorsal spines						
2e	36.5	13	7	13	6	
3e	36.6	15	9	14	7	
3g	36.5	15	6	15	8	
Subtotal		43	22	42	21	0.01
X^2 between dorsal variants		0.28		0.01		
Total (6 replicates)		85	48	85	42	0.85

Experiment Number	Prey Mean SL(mm)	With Morph		Without Morph		Hyper. X^2
		# Offer	# Ate	# Offer	# Ate	
c) Large prey fish						
5 dorsal spines						
5e	44.0	13	4	13	9	
1g	47.8	15	7	15	9	
5g	42.9	15	7	15	8	
Subtotal		43	18	43	26	2.94
6 dorsal spines						
6e	43.4	14	7	14	8	
2g	45.8	15	6	12	7	
6g	43.1	15	8	15	7	
Subtotal		44	21	41	22	0.29
X^2 between dorsal variants		0.11		0.11		
Total (6 replicates)		87	39	84	48	2.58
No cover vegetation present:						
a) Small prey fish						
5 dorsal spines						
1g	29.0	14	8	13	4	
5a	27.2	15	6	14	9	
Subtotal		29	14	27	13	0.00
6 dorsal spines						
2a	26.7	15	5	15	9	
6a	29.3	15	7	14	7	
Subtotal		30	12	29	16	1.34
X^2 between dorsal variants		0.16		0.09		
Total (4 replicates)		59	26	56	29	0.08

Experiment Number	Prey Mean SL(mm)	With Morph		Without Morph		Hyper. X^2
		# Offer	# Ate	# Offer	# Ate	
b) Medium prey fish						
5 dorsal spines						
4h	37.7	15	7	15	7	0.00
6 dorsal spines						
3a	33.1	15	5	15	8	
5h	37.7	15	9	15	6	
1i	37.5	15	8	15	9	
4i	37.3	15	8	15	6	
Subtotal		60	30	60	29	0.03
X^2 between dorsal variants		0.01		0.01		
Total (5 replicates)		75	37	75	36	0.03
c) Large prey fish						
5 dorsal spines						
2i		15	9	15	7	
2j		15	7	14	6	
Subtotal		30	16	29	13	0.42
6 dorsal spines						
3i		14	6	14	7	
4j		14	7	14	6	
Subtotal		28	13	28	13	0.00
X^2 between dorsal variants		0.09		0.00		
Total (4 replicates)		58	29	57	26	0.22

Table 36: Predation by pike on the altered pelvic morphs (i.e. withs clipped). No cover vegetation provided.

		With Morph		Without Morph		
Experiment Number	Prey Mean SL(mm)	# Offer	# Ate	# Offer	# Ate	Hyper. X^2
a) Medium prey fish						
5 dorsal spines						
1f	36.8	15	9	15	6	
2f	36.8	14	8	15	6	
5f	37.2	15	9	15	6	
Subtotal		44	26	45	18	3.21
6 dorsal spines						
4f	36.7	15	9	15	7	
3j	37.6	15	12	15	4	
1j	37.7	14	7	14	6	
Subtotal		44	28	44	17	5.44 **
X^2 between dorsal variants		0.03		0.00		
Total (6 replicages)		88	54	89	35	8.55 ***
b) Large prey fish						
5 dorsal spines						
3f	44.4	15	6	14	8	
6 dorsal spines						
6f	42.9	13	6	15	7	
6k	45.0	15	6	15	8	
Subtotal		28	12	30	15	0.29
X^2 between dorsal variants		0.01		0.31		
Total (3 replicates)		43	18	44	23	0.93

Table 37: Predation by pike on normal and altered with morphs.
No cover vegetation provided.

Experiment Number	Prey Mean SL(mm)	Normal With # Offer	Normal With # Ate	Clipped With # Offer	Clipped With # Ate	Hyper. X^2
a) Medium prey fish						
5 dorsal spines						
1k	37.5	15	5	15	9	2.07
6 dorsal spines						
4k	38.1	15	6	15	8	0.52
X^2 between dorsal variants		0.07		0.04		
Total (2 replicates)		30	11	30	17	2.37
b) Large prey fish						
5 dorsal spines						
2k	45.1	15	7	15	8	0.13
6 dorsal spines						
3k	44.6	15	8	15	6	0.52
X^2 between dorsal variants		0.04		0.19		
Total (2 replicates)		30	15	30	14	0.07

Table 38: Predation marks on surviving fish, unaltered morphs.

Experiment Number	With Morph Survivors Unmarked	With Morph Survivors Marked	Without Morph Survivors Unmarked	Without Morph Survivors Marked	Hyper. X^2
Cover vegetation present:					
a) Small prey fish					
5 dorsal spines					
1b	5	0	4	0	
4b	9	0	9	0	
5b	9	0	8	0	
4c	10	0	7	0	
5c	7	0	8	0	
Subtotal	44	0	36	0	0.00
6 dorsal spines					
2b	8	0	9	0	
3c	8	0	9	0	
Subtotal	16	0	18	0	0.00
X^2 between dorsal variants	0.00		0.00		
Total	60	0	54	0	0.00
b) Medium prey fish					
5 dorsal spines					
1c	2	0	6	0	
4e	6	0	8	0	
4g	8	0	8	0	
Subtotal	16	0	22	0	0.00
6 dorsal spines					
2e	6	0	7	0	
3e	6	0	7	0	
3g	9	0	7	0	
Subtotal	21	0	21	0	0.00
X^2 between dorsal variants	0.00		0.00		
Total	37	0	43	0	0.00

Experiment Number	With Morph Survivors		Without Morph Survivors		Hyper. X^2
	Unmarked	Marked	Unmarked	Marked	
c) Large prey fish					
5 dorsal spines					
5e	9	0	4	0	
1g	6	2	5	1	
5g	7	1	7	0	
Subtotal	22	3	16	1	0.52
6 dorsal spines					
6e	7	0	6	0	
2g	7	2	4	1	
6g	4	3	7	1	
Subtotal	18	5	17	2	1.36
X^2 between dorsal variants	0.83		0.25		
Total	40	8	33	4	1.66
No cover vegetation:					
a) Small prey fish					
5 dorsal spines					
1a	6	0	9	0	
5a	9	0	5	0	
Subtotal	15	0	14	0	0.00
6 dorsal spines					
2a	10	0	6	0	
6a	8	0	7	0	
Subtotal	18	0	13	0	0.00
X^2 between dorsal variants	0.00		0.00		
Total	33	0	27	0	0.00

Experiment Number	With Morph Survivors		Without Morph Survivors		Hyper. X^2
	Unmarked	Marked	Unmarked	Marked	
b) Medium prey fish					
5 dorsal spines					
4h	7	1	8	0	1.14
6 dorsal spines					
3a	10	0	7	0	
5h	6	0	9	0	
1i	7	0	6	0	
4i	7	0	9	0	
Subtotal	30	0	31	0	0.00
X^2 between dorsal variants	3.33_1		0.00		
Total	37	1	39	0	1.05
c) Large prey fish					
5 dorsal spines					
2i	3	3	7	1	
2j	6	2	7	1	
Subtotal	9	5	14	2	4.22 *
6 dorsal spines					
3i	5	3	5	2	
4j	6	1	7	1	
Subtotal	11	4	12	3	0.33
X^2 between dorsal variants	0.20		0.33		
Total	20	9	26	5	3.47

Table 39: Predation marks on surviving fish, altered with and normal without morphs.

	Clipped With Morph Survivors		Without Morph Survivors		Hyper.
Experiment Number	Unmarked	Marked	Unmarked	Marked	X^2
a) Medium prey fish					
5 dorsal spines					
1f	5	1	9	0	
2f	5	1	8	1	
5f	6	0	9	0	
Subtotal	16	2	26	1	1.09
6 dorsal spines					
4f	4	2	8	0	
3j	3	0	10	1	
1j	7	0	8	0	
Subtotal	14	2	26	1	1.39
X^2 between dorsal variants	0.02		0.00		
Total	30	4	52	2	2.49
b) Large prey fish					
5 dorsal spines					
3f	7	2	6	0	1.87
6 dorsal spines					
6f	4	3	6	2	
6k	6	3	6	1	
Subtotal	10	6	12	3	2.64
X^2 between dorsal variants	0.62		1.39		
Total	17	8	18	3	3.64

Table 40: Predation marks on normal with, altered with morphs.

Experiment Number	Normal With Morph Survivors		Clipped With Morph Survivors		Hyper. X^2
	Unmarked	Marked	Unmarked	Marked	
a) Medium prey fish					
5 dorsal spines					
1k	8	2	5	1	0.02
6 dorsal spines					
4k	8	1	7	0	0.87
X^2 between dorsal variants	0.00_1		0.04_1		
Total	16	3	12	1	0.59
b) Large prey fish					
5 dorsal spines					
2k	6	2	4	3	1.50
6 dorsal spines					
3k	3	4	3	6	0.50
X^2 between dorsal variants	0.55_1		0.20_1		
Total	9	6	7	9	0.70

Table 41: Attacks on the pelvic morphs (unaltered morphs).

Experiment Number	With Morph # Offered	 # Attacked	Without Morph # Offered	 # Attacked	Hyper. X^2
Cover vegetation present:					
a) Small prey fish no marks ∴attacks = consumed table					
b) Medium prey fish no marks ∴attacks = consumed table					
c) Large prey fish					
5 dorsal spines					
5e	13	4	13	9	
1g	15	9	15	10	
5g	15	8	15	8	
Subtotal	43	21	43	27	1.68
6 dorsal spines					
6e	14	7	14	8	
2g	15	8	12	8	
6g	15	11	15	8	
Subtotal	44	26	41	24	0.00
X^2 between dorsal variants	0.27		0.04		
Total	87	47	84	51	0.78
No cover vegetation present:					
a) Small prey fish no marks ∴attacks = consumed table.					
b) Medium prey fish					
5 dorsal spines					
4h	15	8	15	7	0.13
(all other medium experiments - no marks ∴attacks = consumed table)					

Experiment Number	With Morph # Offered	 # Attacked	Without Morph # Offered	 # Attacked	Hyper. X^2
c) Large prey fish					
5 dorsal spines					
2i	15	12	15	8	
2j	15	9	14	7	
Subtotal	30	21	29	15	2.03
6 dorsal spines					
3i	14	9	14	9	
4j	14	8	14	7	
Subtotal	28	17	28	16	0.07
X^2 between dorsal variants	0.18		0.05		
Total	58	38	57	31	1.47

Table 42: Attacks on pelvic morphs (altered with morphs, normal withouts).

	Clipped With Morph		Normal Without Morph		
Experiment Number	# Offered	# Attacked	# Offered	# Attacked	Hyper. X^2
a) Medium prey fish					
5 dorsal spines					
1f	15	10	15	6	
2f	14	9	15	7	
5f	15	9	15	6	
Subtotal	44	28	45	19	4.05 *
6 dorsal spines					
4f	15	11	15	7	
3j	15	12	15	5	
1j	14	7	14	6	
Subtotal	44	30	44	18	6.53 **
X^2 between dorsal variants	0.04		0.00		
Total	88	58	89	37	10.45 ***
b) Large prey fish					
5 dorsal spines					
3f	15	8	11	8	0.04
6 dorsal spines					
6f	13	9	15	9	
6k	15	9	15	9	
Subtotal	28	18	30	18	0.11
X^2 between dorsal variants	0.12		0.01		
Total	43	26	44	26	0.02

Table 43: Attacks on normal with, altered with morphs.

Experiment Number	Normal With Morph # Offered	 # Attacked	Clipped With Morph # Offered	 # Attacked	Hyper. X^2
a) Medium prey fish					
5 dorsal spines					
1k	15	7	15	10	1.18
6 dorsal spines					
4k	15	7	15	8	0.13
X^2 between dorsal variants	0.00		0.14		
Total	30	14	30	18	1.05
b) Large prey fish					
5 dorsal spines					
2k	15	9	15	11	0.58
6 dorsal spines					
3k	15	12	15	12	0.00
X^2 between dorsal variants	0.25		0.02		
Total	30	21	30	23	0.33

Table 44: Lethocerus americanus (adults or nymph) predation on pelvic morphs.

Experiment Number	Prey Mean SL(mm)	With Morph # Offer	With Morph # Ate	Without Morph # Offer	Without Morph # Ate	Hyper. X^2
a) Small prey size						
5 dorsal spines						
12a adult	22.8	7	2	7	6	
16c adult	26.6	7	6	7	2	
13c adult	27.4	7	3	7	3	
14d adult	24.9	6	2	6	3	
18d adult	28.1	7	2	7	3	
15b nymph	25.9	7	4	7	4	
12c nymph	27.6	7	2	7	5	
15c nymph	26.4	7	3	7	4	
11c nymph	24.9	7	5	7	4	
14c nymph	24.4	7	4	7	3	
Subtotal		69	33	69	37	0.24
6 dorsal spines						
16a	20.5	7	1	4	3	3.69
X^2 between dorsal variants		0.59_1		0.00_1		
Total (11 replicates)		76	34	73	40	1.50
b) Medium prey size						
5 dorsal spines						
13b adult	32.7	7	5	7	2	
15d adult	32.8	7	2	7	5	
17d adult	30.8	6	4	6	3	
Subtotal		20	11	20	10	0.10
6 dorsal spines						
16d	30.1	7	4	6	3	0.06
X^2 between dorsal variants		0.06_1		0.00		
Total (4 replicates)		27	15	26	13	0.16

Table 45: Dytiscus sp. predation on pelvic morphs.

Experiment Number	Prey Mean SL(mm)	With Morph # Offer	With Morph # Ate	Without Morph # Offer	Without Morph # Ate	Hyper. X^2
a) Small prey size						
5 dorsal spines						
13a	22.1	7	4	7	3	
14a	25.9	7	4	7	2	
15a	26.6	7	4	7	2	
12b	28.3	7	5	7	2	
14b	27.1	7	4	7	3	
17b	28.3	7	4	7	3	
11d	27.6	7	4	7	2	
Total (7 replicates)		49	29	49	17	5.84 **
6 dorsal spines						
11a	22.7	7	5	6	3	
18b	27.9	7	4	7	4	
16b	27.6	7	3	7	4	
17c	24.1	7	4	7	3	
18c	27.2	7	5	7	3	
Total (5 replicates)		35	21	34	21	0.02
b) Medium prey size						
11b	32.2	7	3	7	4	0.27

Table 46: Prey and pike sizes in predation experiments.

Experiment Conditions	Predator Mean SL(mm)	Prey Mean SL(mm)	Range of Prey SL(mm)	Predator/ Prey SL Ratio
Intact prey fish				
Cover:				
small	126.7	25.0	20-29.9	5.1
medium	152.6	35.4	30-39.9	4.3
large	160.5	44.5	40-49.9	3.6
No cover:				
small	123.0	29.1	21-29.9	4.2
medium	149.6	36.7	35-39.9	4.1
large	159.5	44.6	40-49.9	3.6
Altered prey fish				
Clip with/normal without:				
medium	149.7	37.1	35-39.9	3.9
large	162.1	44.1	40-49.9	3.7
Clip with/normal with:				
medium	148.0	37.8	35-39.9	3.9
large	161.9	44.9	41-50.0	3.6
1976 Experiments:				
Wakomao Lake	147.8	39.6	31-50.0	3.8
Fairydell Creek	140.0	42.5	?	3.3
Whitemud Creek	166.3	51.0	40-70.0	3.3

APPENDIX 5

Pike and Stickleback Body Measurements

The influence of predator to prey size (length) ratio for northern pike has been investigated by Frost (1954) and Mauck and Coble (1971) as well as Christiansen (1976). The latter author suggests that length of prey is not the most critical measure determining the size of prey consumed. Rather, Christiansen (p. 59) suggests that since the prey are turned on their side before ingestion "the critical relationship, determining maximum size of prey consumed, is that between maximum jaw width of the predator and maximum body depth of prey fish". The maximum body depth (including dorsal and pelvic spines when present) of sticklebacks can vary considerably. The relationship between the variation and morph type, and that between pike jaw width and standard length was investigated in the Wakomao Lake fish.

Methods

Predator standard length and jaw width were taken on the samples of pike obtained for stomach analysis and two small young of year pike taken in the Redwater River (Figure 1, site 5). Standard length was measured to the nearest 0.5 cm with a meter stick according to the usual method (Hubbs and Lagler, 1974). Jaw width was taken, to the nearest 0.1 cm with a plastic ruler inserted in the back of the closed mouth, as the inside distance between the premaxillary wings.

Stickleback standard length was taken as before. Total body depth (TBD) of each morph was taken as the shortest distance between the tip of the erect second dorsal spine and the erect, ventral most pelvic spine in the with morphs; and the tip of the erect second dorsal spine and the most ventral point of the belly in the without morphs. In both cases this measure was made perpendicular to the long axis of the body read on a calibrated eye piece micrometer of a dissecting microscope at 10X.

The jaw width and TBD data points in each standard length unit (1 cm) were averaged and a least squares linear regression equation and correlation coefficient (r) calculated.

Results

Table 47 presents the averaged jaw width for each pike standard length category. Figure 9 shows the regression line for this data. Table 48 presents the TBD results for each stickleback morph. Figure 10 shows the calculated regression lines.

Using the regression equations to calculate the average TBD for the mean size of stickleback presented in each size group in the predation experiments one obtains:

25 mm SL	with	0.70	cm TBD
	without	0.59	" "
35 mm SL	with	0.92	" "
	without	0.81	" "
45 mm SL	with	1.14	" "
	without	1.03	" "

The first observation is that the pelvic morphs do not differ greatly in their TBD (Figure 10).

These sticklebacks are consumed by pike (11-18 cm in standard length) with a jaw width of 1.02-1.55 cm. It is clear that some prey items of both morphs exceed the minimal jaw width of the pike thus making them unavailable as prey and enhancing their ability to escape.

Discussion

In the experiments performed with pike it is probable that both morphs in the large size category exceeded a critical size which the pike could easily ingest. This would result in a lack of selective predation as observed. The results would suggest that once pike reached a certain size (i.e. about 20-25 cm SL) their jaw width exceeds the TBD of most sticklebacks and any selective predation would not be due to the morphological difference (see stomachs section). A corollary of this would be a very low escape rate when attacked by large pike in the lake situation and a much higher escape rate when attacked by small pike in the predation experiments. Both conditions were observed in the present study.

Table 47: Jaw width measurements for standard length categories of Wakomao Lake pike.

Mean Standard Length (cm)	Number of Measurements	Mean Jaw Width (cm)	Standard Deviation
7.9 *	1	0.90	--
9.8 *	1	0.95	--
17.4	2	1.75	0.07
18.3	4	1.65	0.25
19.4	10	1.84	0.16
20.2	11	1.85	0.22
21.5	1	1.80	--
22.5	4	2.07	0.27
23.4	7	1.91	0.31
24.5	6	2.13	0.24
25.4	27	2.17	0.20
26.4	17	2.18	0.23
27.4	5	2.28	0.16
41.0	1	5.80	--
42.3	2	3.70	0.42
43.0	1	3.70	--
44.5	1	3.60	--
45.3	3	4.30	0.36
46.3	3	3.93	0.40
47.5	5	4.30	0.34
49.5	1	4.10	--
50.0	1	4.20	--
51.3	2	4.40	0.14
54.0	1	5.60	--
55.0	1	5.00	--
57.0	1	4.30	--
58.0	1	4.30	--
63.0	1	6.80	--

* Redwater River pike

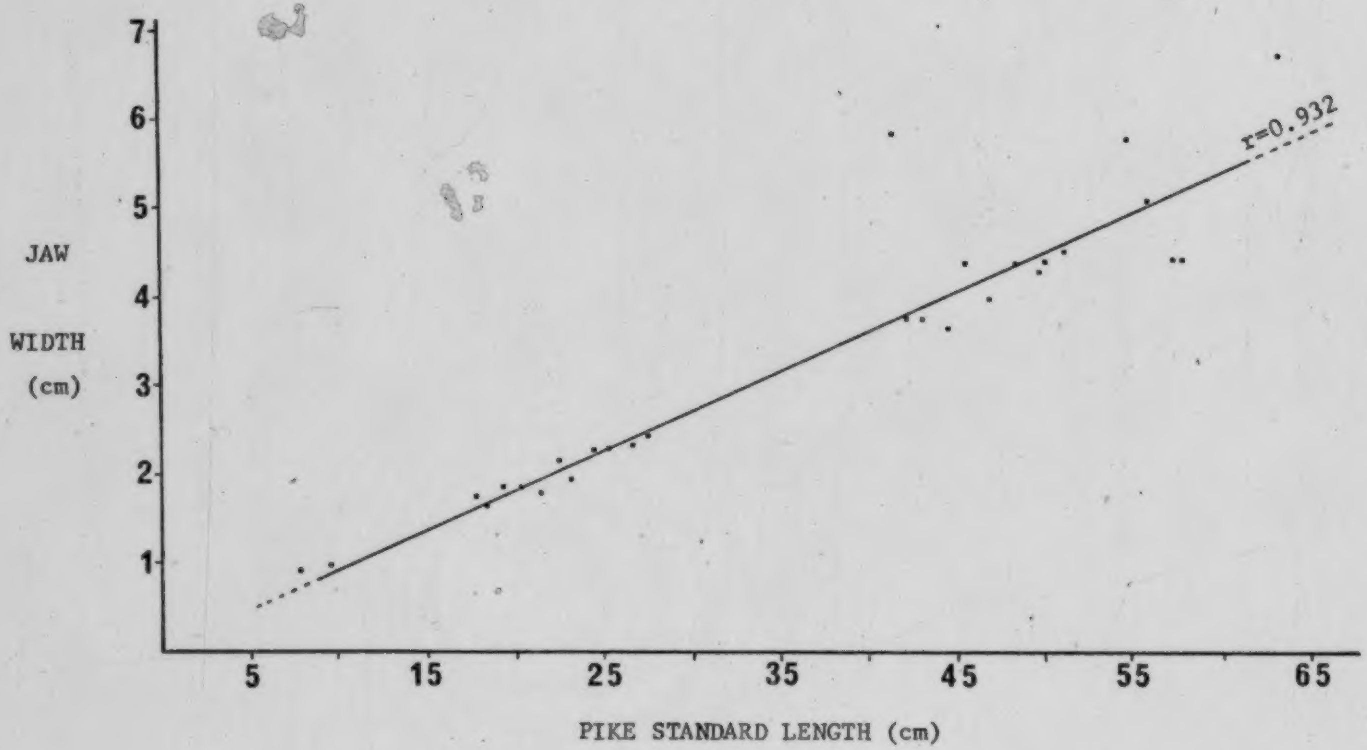


Figure 9: Regression analysis of the relationship between pike jaw width and standard length. Least squares Model 1 linear regression used.

Regression Equation: Jaw Width = 0.033 + 0.0895 Standard Length.

Table 48: Total body depth (TBD) measurements for sticklebacks from Wakomao Lake (collection 76-4).

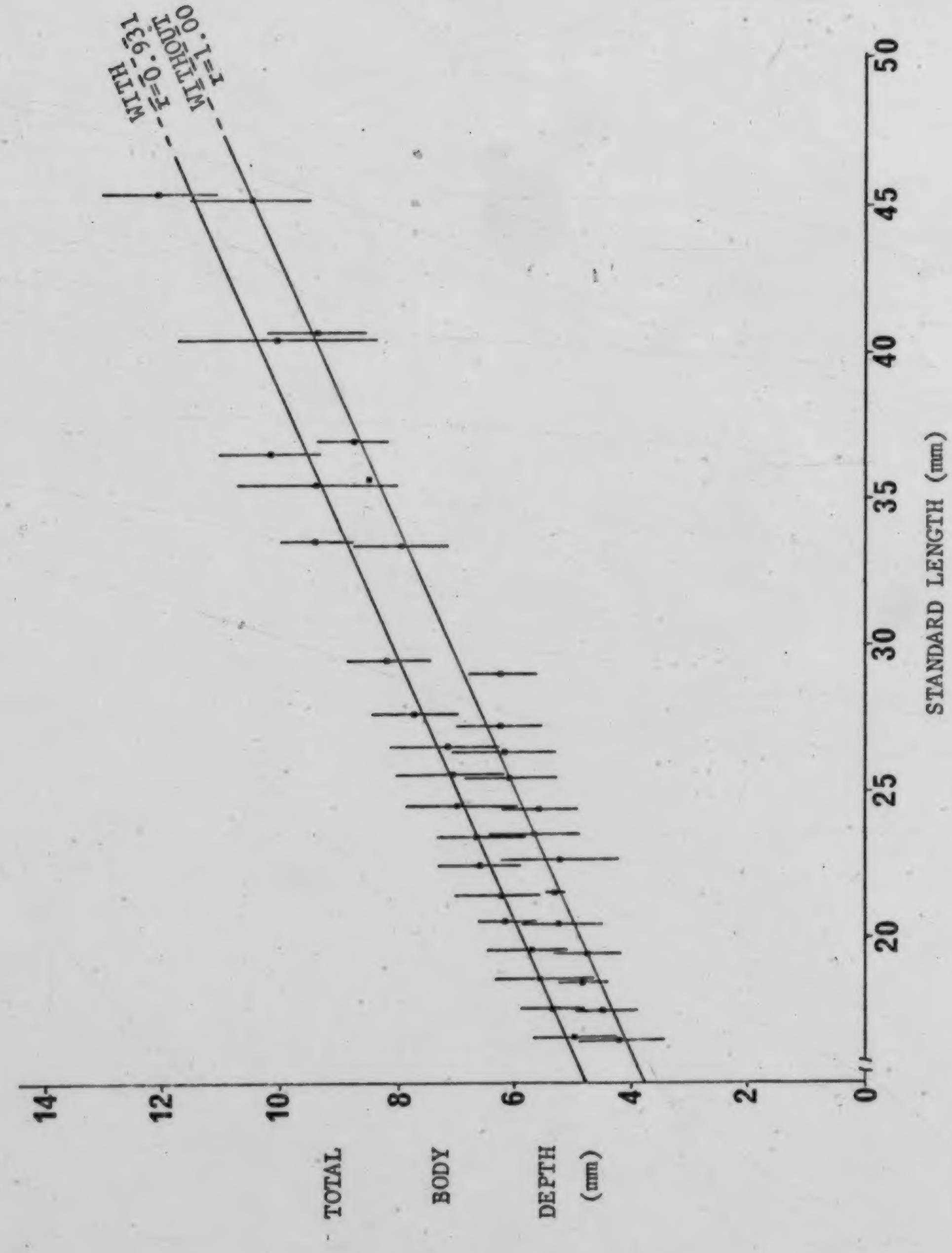
Mean SL (mm)	Mean TBD (mm)	Standard Deviation	Mean SL (mm)	Mean TBD (mm)	Standard Deviation
with morph n = 324			without morph n = 111		
15.4	4.3	0.265	15.8	4.0	--
16.6	4.9	0.329	16.6	4.2	0.349
17.5	5.3	0.264	17.5	4.4	0.251
18.5	5.5	0.384	18.5	4.8	0.210
19.5	5.7	0.332	19.4	4.7	0.281
20.5	6.1	0.251	20.4	5.2	0.347
21.4	6.2	0.308	21.5	5.3	0.058
22.4	6.5	0.362	22.6	5.2	0.503
23.4	6.6	0.370	23.5	5.6	0.369
24.4	6.9	0.467	24.4	5.5	0.338
25.5	7.0	0.498	25.5	6.0	0.378
26.5	7.1	0.486	26.3	6.2	0.427
27.6	7.7	0.365	28.4	6.2	--
28.4	7.8	0.232	27.2	6.2	0.346
29.4	8.1	0.358	29.0	6.2	0.289
30.3	8.3	0.473	30.5	6.9	--
31.4	8.7	0.645	31.0	7.2	--
32.5	9.2	0.306	32.3	7.5	--
33.5	9.3	0.306	33.3	7.9	0.395
34.4	8.9	0.400	35.5	8.4	0.000
35.4	9.3	0.685	36.8	8.7	0.283
36.5	10.1	0.473	37.0	8.2	--
37.4	10.1	0.321	39.3	9.8	--
38.6	10.3	0.288	40.6	9.3	0.421
39.3	10.1	0.665	41.8	9.5	--
40.4	10.0	0.850	42.6	10.3	0.354
41.4	11.1	0.289	45.1	10.5	0.495
42.8	10.0	--	52.5	11.7	--
43.5	10.7	1.180			
44.7	10.9	0.354			
45.3	12.1	0.495			
46.7	11.5	--			
51.7	13.1	--			
53.4	12.9	--			

Figure 10: Regression analysis of the relationship between total body depth (TBD) and standard length of stickleback pelvic morphs, with and without. Mean shown ± 2 S.D. Least squares Model 1 linear regression used.

Regression Equations:

with - TBD = 1.479 + 0.221 Standard Length

without - TBD = 0.482 + 0.219 Standard Length


WITH
r̄=0.931
WITHOUT
r=1.00
TOTAL
BODY
DEPTH
(mm)
0
2
4
6
8
10
12
14
20
25
30
35
40
45
50
STANDARD LENGTH (mm)

APPENDIX 6

Behaviour Results and Analysis

Behaviour Variable Key:

Table 49 1 = total activity
2 = jerky swimming
3 = sculling
4 = fast swimming
5 = frozen
6 = in cover
7 = in vegetation
8 = dorsal spines erect

Table 50 9 = survival time (minutes)
10 = manipulation time (minutes)
11 = time to first orientation (minutes)
12 = retreats (normalized % of total for that morph)
13 = jumps (normalized % of total for that morph)

Table 49: Percentage (normalized) of time spent in various behaviours, pike experiments.

	Behaviour Variables							
	1	2	3	4	5	6	7	8
Small prey fish, with morph								
baseline								
	00.0	00.0	00.0	00.0	90.0	90.0	90.0	00.0
	90.0	48.0	00.0	42.0	00.0	20.3	00.0	32.8
	90.0	51.5	11.5	36.1	00.0	23.0	00.0	56.3
	90.0	63.9	17.8	18.4	00.0	48.0	00.0	51.5
	90.0	00.0	90.0	00.0	00.0	00.0	00.0	00.0
	90.0	35.2	28.9	41.1	00.0	41.1	00.0	00.0
	73.6	22.0	44.6	32.4	16.4	12.5	00.0	00.0
	90.0	56.3	32.8	06.5	00.0	00.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	04.8	00.0	34.9
	62.0	35.2	42.0	00.0	28.0	20.3	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	33.7	00.0	85.2
	90.0	90.0	00.0	00.0	00.0	10.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	04.8	00.0	00.0
	71.6	00.0	52.4	31.5	18.4	38.8	00.0	19.1
$\overline{X}$	79.1	48.0	22.9	14.9	10.9	24.8	06.4	20.0
S.D.	24.5	34.3	27.2	17.7	24.5	24.5	24.1	27.9
predator								
	00.0	00.0	00.0	00.0	90.0	90.0	90.0	00.0
	90.0	00.0	00.0	90.0	00.0	00.0	00.0	00.0
	90.0	30.0	60.0	00.0	00.0	90.0	00.0	00.0
	90.0	00.0	90.0	00.0	00.0	90.0	00.0	54.8
	69.9	00.0	69.9	20.1	00.0	20.1	00.0	53.5
	20.7	00.0	14.5	14.5	69.3	00.0	00.0	00.0
	90.0	45.0	45.0	00.0	00.0	00.0	00.0	00.0
	90.0	39.2	50.8	00.0	00.0	00.0	00.0	45.0
	90.0	45.0	00.0	45.0	00.0	00.0	00.0	45.0
	90.0	35.2	54.8	00.0	00.0	00.0	00.0	00.0
	90.0	35.2	54.8	00.0	00.0	90.0	00.0	90.0
	90.0	90.0	00.0	00.0	00.0	00.0	00.0	00.0
	90.0	00.0	90.0	00.0	00.0	00.0	00.0	00.0
	16.4	00.0	15.7	04.8	73.6	71.6	00.0	90.0
$\overline{X}$	71.9	22.8	39.0	12.5	16.6	32.3	06.4	27.0
S.D.	33.0	27.4	33.4	25.7	33.3	42.4	24.1	35.0

	Behaviour Variables							
	1	2	3	4	5	6	7	8
Small prey fish, without morph								
baseline								
	90.0	70.4	20.5	00.0	00.0	30.2	00.0	23.0
	79.5	08.1	76.7	00.0	10.5	18.4	00.0	30.2
	74.3	00.0	30.2	55.1	15.7	20.9	00.0	00.0
	46.5	00.0	46.5	00.0	43.5	35.7	00.0	43.9
	90.0	90.0	00.0	00.0	00.0	44.3	00.0	15.0
	90.0	13.3	00.0	76.7	00.0	50.8	00.0	00.0
	90.0	00.0	90.0	00.0	00.0	49.2	00.0	66.4
	31.9	21.4	22.5	00.0	58.1	00.0	00.0	54.8
	90.0	65.4	20.3	13.3	00.0	10.5	00.0	16.4
	90.0	52.7	36.5	06.5	00.0	00.0	00.0	18.4
	28.9	17.1	22.5	00.0	61.1	65.9	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	25.6	00.0	28.5
$\overline{X}$	74.3	35.7	30.5	12.6	15.7	29.3	00.0	24.7
S.D.	24.1	28.7	28.7	25.6	24.1	20.7	00.0	21.5
predator								
	90.0	57.0	41.8	00.0	00.0	00.0	00.0	37.5
	90.0	35.1	54.8	00.0	00.0	00.0	00.0	40.9
	90.0	00.0	40.9	49.1	00.0	00.0	00.0	00.0
	11.5	00.0	09.5	06.5	78.5	00.0	00.0	61.1
	90.0	21.4	68.6	00.0	00.0	79.5	00.0	71.6
	90.0	26.6	56.8	18.4	00.0	18.4	00.0	56.8
	26.6	00.0	26.6	00.0	63.4	00.0	00.0	90.0
	10.6	00.0	10.6	79.4	00.0	00.0	00.0	00.0
	90.0	35.1	54.8	00.0	00.0	00.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	00.0	00.0	00.0
	34.2	00.0	34.2	00.0	55.8	00.0	00.0	00.0
	90.0	29.0	61.0	00.0	00.0	00.0	00.0	17.9
$\overline{X}$	66.9	24.5	38.3	12.8	16.5	08.1	00.0	31.3
S.D.	34.6	28.0	22.5	25.5	30.2	23.1	00.0	32.8

	Behaviour Variables							
	1	2	3	4	5	6	7	8
Medium prey fish, with morph								
baseline								
	58.9	00.0	58.9	00.0	31.1	59.8	00.0	90.0
	34.5	00.0	34.5	00.0	55.5	90.0	00.0	90.0
	38.1	25.1	26.6	00.0	51.9	46.9	26.1	47.7
	54.3	37.3	32.8	00.0	35.7	90.0	00.0	34.9
	04.8	00.0	04.8	00.0	85.2	90.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	79.5	00.0	55.1
	90.0	00.0	90.0	00.0	00.0	90.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	29.3	00.0	17.8
	40.4	09.5	38.8	00.0	49.6	77.5	00.0	00.0
	00.0	00.0	00.0	00.0	90.0	00.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	29.3	00.0	46.1
	90.0	90.0	00.0	00.0	00.0	00.0	00.0	81.9
	90.0	90.0	00.0	00.0	00.0	70.9	00.0	37.3
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	90.0
	29.8	29.8	00.0	00.0	60.2	90.0	60.2	90.0
$\overline{X}$	53.4	36.8	19.1	00.0	36.6	62.2	05.7	45.4
S.D.	35.3	40.7	27.5	00.0	35.3	33.1	16.5	36.4
predator								
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	90.0
	19.1	00.0	19.1	00.0	70.9	62.5	00.0	90.0
	15.0	00.0	15.0	00.0	75.0	90.0	00.0	90.0
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	90.0
	10.8	00.0	07.7	07.7	79.2	90.0	00.0	16.2
	31.4	00.0	30.9	05.1	58.6	90.0	26.0	90.0
	06.5	00.0	06.5	00.0	83.5	90.0	00.0	00.0
	15.0	08.1	09.5	00.0	75.0	81.9	75.0	81.9
	08.1	08.1	00.0	00.0	81.9	90.0	00.0	79.5
	00.0	00.0	00.0	00.0	90.0	00.0	00.0	90.0
	12.5	10.5	06.8	00.0	77.5	79.5	61.1	90.0
	12.7	10.9	00.0	06.3	77.3	81.1	81.1	90.0
	10.5	10.5	00.0	00.0	79.5	90.0	58.9	83.5
	23.3	00.0	21.7	08.1	66.7	90.0	11.4	90.0
	00.0	00.0	00.0	00.0	90.0	90.0	43.5	90.0
$\overline{X}$	11.0	03.2	07.8	01.8	79.0	80.3	23.8	77.4
S.D.	09.2	04.7	09.8	03.2	09.2	23.5	31.2	28.5

	Behaviour Variables							
	1	2	3	4	5	6	7	8
Medium prey fish, without morph								
baseline								
	90.0	74.3	15.7	00.0	00.0	53.5	00.0	76.7
	90.0	83.5	06.5	00.0	00.0	09.3	00.0	37.6
	56.8	46.1	25.1	00.0	33.2	13.3	00.0	48.5
	00.0	00.0	00.0	00.0	90.0	00.0	00.0	74.7
	31.1	00.0	31.1	00.0	58.9	90.0	22.5	90.0
	61.1	61.1	00.0	00.0	28.9	38.5	34.5	42.0
	90.0	64.9	25.1	00.0	00.0	26.1	00.0	90.0
	00.0	00.0	00.0	00.0	90.0	00.0	00.0	00.0
	90.0	50.0	40.0	00.0	00.0	42.3	00.0	31.5
	12.5	00.0	12.5	00.0	77.5	90.0	00.0	90.0
	43.9	31.1	27.5	00.0	46.1	90.0	34.5	73.6
	28.9	19.1	20.9	00.0	61.1	90.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	11.5	00.0	44.3
	58.9	49.6	23.0	00.0	31.1	06.5	00.0	12.5
	90.0	41.1	48.9	00.0	00.0	55.5	00.0	51.2
$\overline{X}$	55.5	40.7	18.4	00.0	34.5	41.1	06.1	50.8
S.D.	34.5	31.4	15.3	00.0	34.5	35.2	12.9	31.3
predator								
	90.0	00.0	90.0	00.0	00.0	90.0	00.0	90.0
	08.1	00.0	08.1	00.0	81.9	90.0	00.0	90.0
	90.0	32.7	56.2	07.7	00.0	70.7	00.0	82.3
	00.0	00.0	00.0	00.0	90.0	00.0	00.0	90.0
	00.0	00.0	00.0	00.0	90.0	90.0	90.0	90.0
	00.0	00.0	00.0	00.0	90.0	90.0	90.0	90.0
	90.0	52.2	30.0	20.7	00.0	00.0	00.0	90.0
	00.0	00.0	00.0	00.0	90.0	00.0	00.0	00.0
	30.5	00.0	30.5	00.0	59.5	13.8	00.0	76.2
	09.5	00.0	00.0	09.5	80.5	83.2	00.0	90.0
	00.0	00.0	00.0	00.0	90.0	90.0	90.0	90.0
	08.3	00.0	00.0	08.3	81.7	90.0	00.0	08.3
	10.8	10.8	00.0	00.0	80.9	90.0	00.0	77.2
	90.0	00.0	90.0	00.0	00.0	00.0	00.0	00.0
	90.0	33.7	56.3	00.0	00.0	38.3	00.0	00.0
$\overline{X}$	34.5	08.6	24.1	03.1	55.6	55.7	18.0	64.3
S.D.	41.3	16.7	33.5	06.0	41.4	41.1	37.3	39.1

	Behaviour Variables							
	1	2	3	4	5	6	7	8
Large prey fish, with morph								
baseline								
	80.7	54.3	33.2	00.0	09.3	41.1	10.3	74.2
	29.3	00.0	29.3	00.0	60.7	17.8	00.0	32.8
	90.0	00.0	90.0	00.0	00.0	00.0	00.0	30.2
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	00.0
	90.0	37.2	52.8	00.0	00.0	31.5	00.0	00.0
	74.2	39.6	46.1	00.0	15.8	55.9	15.8	75.6
	90.0	90.0	00.0	00.0	00.0	54.7	00.0	83.2
	90.0	90.0	00.0	00.0	00.0	22.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	45.7	00.0	55.9
	90.0	80.4	07.7	00.0	00.0	00.0	00.0	22.0
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	15.7	00.0	00.0
	18.4	18.4	00.0	63.4	43.9	43.4	16.4	00.0
	04.8	04.8	00.0	00.0	80.5	25.5	00.0	00.0
	90.0	90.0	00.0	00.0	00.0	39.6	00.0	44.2
$\bar{X}$	61.8	45.6	17.3	04.2	26.0	38.2	02.8	27.9
S.D.	38.5	39.6	27.5	16.4	36.3	27.2	06.0	31.7
predator								
	90.0	00.0	90.0	00.0	00.0	90.0	47.1	90.0
	00.0	00.0	00.0	00.0	90.0	00.0	00.0	90.0
	90.0	00.0	90.0	00.0	00.0	00.0	00.0	39.2
	24.9	00.0	23.7	07.3	65.1	65.1	00.0	61.7
	16.0	00.0	16.0	00.0	74.0	00.0	00.0	00.0
	00.0	00.0	00.0	00.0	90.0	06.3	06.3	90.0
	69.3	45.0	30.0	20.7	20.7	90.0	00.0	90.0
	90.0	25.3	64.7	00.0	00.0	00.0	00.0	52.9
	07.7	04.4	06.3	00.0	82.3	85.6	00.0	90.0
	28.1	00.0	28.1	00.0	61.9	00.0	00.0	65.7
	38.7	00.0	38.7	00.0	51.3	90.0	27.8	68.8
	14.3	11.5	08.1	00.0	75.7	78.3	00.0	78.3
	23.8	00.0	23.8	00.0	66.2	66.2	29.7	00.0
	17.5	00.0	17.5	00.0	72.4	90.0	17.5	25.3
	90.0	90.0	00.0	00.0	00.0	90.0	00.0	00.0
$\bar{X}$	40.0	11.7	29.1	01.9	50.0	50.1	08.6	56.1
S.D.	35.3	25.1	30.1	05.5	35.3	42.2	14.9	35.1

	Behaviour Variables							
	1	2	3	4	5	6	7	8
Large prey fish, without morph								
baseline								
	90.0	90.0	00.0	00.0	00.0	00.0	00.0	30.2
	90.0	90.0	00.0	00.0	00.0	33.6	00.0	40.0
	90.0	90.0	00.0	00.0	00.0	42.7	00.0	70.3
	49.6	39.2	25.1	00.0	40.4	21.1	00.0	81.9
	90.0	90.0	00.0	00.0	00.0	41.1	00.0	82.7
	90.0	54.3	41.5	00.0	00.0	47.3	23.6	00.0
	78.5	63.4	23.6	00.0	11.5	39.6	00.0	49.0
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	90.0
	90.0	90.0	00.0	00.0	00.0	12.4	00.0	00.0
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	78.8
	90.0	90.0	00.0	00.0	00.0	80.4	00.0	90.0
	73.6	36.5	48.9	00.0	16.4	17.1	00.0	32.3
	90.0	90.0	00.0	00.0	00.0	25.5	00.0	30.7
	90.0	90.0	00.0	00.0	00.0	30.3	00.0	00.0
	90.0	12.4	77.6	00.0	00.0	35.7	00.0	00.0
$\overline{X}$	73.4	61.7	14.4	00.0	16.5	40.5	01.6	48.4
S.D.	31.8	35.5	24.2	00.0	31.8	27.1	06.1	37.0
predator								
	09.3	09.3	00.0	00.0	80.7	83.2	80.7	90.0
	10.3	10.3	00.0	00.0	79.7	90.0	00.0	90.0
	17.1	08.1	13.4	04.4	73.6	81.9	21.0	90.0
	11.2	00.0	09.3	05.7	78.8	00.0	00.0	80.7
	90.0	22.2	67.8	00.0	00.0	90.0	90.0	90.0
	00.0	00.0	00.0	00.0	90.0	90.0	90.0	00.0
	90.0	34.0	56.0	00.0	00.0	90.0	00.0	90.0
	00.0	00.0	00.0	00.0	90.0	90.0	00.0	90.0
	12.0	12.0	00.0	00.0	78.0	78.0	00.0	75.1
	23.0	00.0	00.0	23.0	67.0	70.2	00.0	90.0
	90.0	18.7	80.7	09.3	00.0	25.1	00.0	90.0
	13.3	00.0	13.3	00.0	76.7	76.7	00.0	75.2
	26.1	07.5	24.8	00.0	63.9	82.5	00.0	73.1
	56.7	23.5	45.6	00.0	34.5	50.5	00.0	78.6
	45.0	00.0	33.2	26.6	45.0	71.6	00.0	56.8
$\overline{X}$	32.9	09.7	22.9	04.6	57.2	71.3	18.8	77.3
S.D.	33.2	10.7	27.5	08.7	33.1	26.5	35.7	23.5

Table 50: Morph behaviour during pike predator experiments.

	Behaviour Variables				
	9	10	11	12	13
Small prey fish, with morph					
	15.0	--	15.0	00.0	00.0
	00.3	00.0	00.0	00.0	00.0
	00.8	00.0	00.3	00.0	00.0
	00.9	00.3	00.7	00.0	00.0
	01.7	00.1	01.3	00.0	10.6
	03.2	00.0	00.2	00.0	00.0
	00.4	00.0	00.3	00.0	00.0
	01.0	00.0	00.2	00.0	00.0
	00.2	00.0	00.1	00.0	15.2
	00.6	00.0	00.3	00.0	10.6
	00.6	00.0	00.3	45.0	00.0
	00.2	00.0	00.1	45.0	00.0
	00.2	00.0	00.2	00.0	10.6
	15.0	--	00.2	00.0	10.6
$\overline{X}$	02.9	00.0	01.4	06.4	04.1
S.D.	05.2	00.1	03.9	16.3	05.8
Small prey fish, without morph					
	02.7	00.0	01.7	00.0	09.3
	02.1	00.0	00.7	00.0	00.0
	00.7	00.0	00.6	00.0	00.0
	15.0	--	00.7	00.0	13.1
	03.0	00.0	01.7	22.2	00.0
	01.0	00.0	00.2	00.0	13.1
	01.0	00.0	00.1	00.0	00.0
	05.8	00.0	00.4	00.0	09.3
	00.9	00.0	00.5	00.0	00.0
	00.1	00.0	00.0	00.0	00.0
	01.9	00.0	00.5	00.0	00.0
	01.7	00.0	00.2	00.0	13.1
$\overline{X}$	03.0	00.0	00.6	01.9	04.8
S.D.	04.1	00.0	00.5	06.4	06.1

	Behaviour Variables				
	9	10	11	12	13
Medium prey fish, with morph					
	15.0	--	04.1	00.0	00.0
	15.0	00.0	09.7	00.0	10.6
	15.0	--	00.4	00.0	10.6
	15.0	--	00.6	00.0	00.0
	11.3	02.4	03.1	00.0	18.7
	12.5	00.0	01.0	00.0	15.2
	15.0	--	15.0	00.0	00.0
	15.0	--	15.0	00.0	10.6
	15.0	--	01.4	00.0	00.0
	05.9	00.2	04.3	00.0	00.0
	15.0	--	03.4	00.0	10.6
	08.4	00.0	07.5	00.0	15.2
	15.0	--	03.3	00.0	00.0
	05.1	00.1	01.8	00.0	18.7
	15.0	--	06.4	00.0	10.6
$\bar{X}$	12.9	00.5	05.1	00.0	08.1
S.D.	03.5	00.9	04.8	00.0	07.3
Medium prey fish, without morph					
	01.2	00.0	00.9	00.0	00.0
	15.0	--	14.3	00.0	13.1
	05.5	00.0	01.3	00.0	09.3
	14.0	00.2	13.7	00.0	00.0
	15.0	--	15.0	00.0	00.0
	15.0	--	15.0	00.0	00.0
	00.8	00.0	00.4	00.0	13.1
	15.0	--	15.0	00.0	00.0
	03.5	00.1	03.1	00.0	09.3
	07.4	00.0	05.9	00.0	13.1
	15.0	--	12.6	00.0	00.0
	04.8	00.3	03.9	00.0	09.3
	14.2	00.1	12.2	00.0	00.0
	00.4	00.0	00.3	00.0	00.0
	01.3	00.0	00.4	00.0	13.1
$\bar{X}$	08.5	00.1	07.6	00.0	05.3
S.D.	06.3	00.1	06.4	00.0	06.1

	Behaviour Variables				
	9	10	11	12	13
Large prey fish, with morph					
	01.3	00.3	00.4	00.0	00.0
	15.0	--	15.0	00.0	00.0
	00.5	00.1	00.4	00.0	10.6
	06.2	00.5	02.7	00.0	15.2
	09.3	00.8	06.8	00.0	00.0
	15.0	--	11.2	00.0	00.0
	00.8	00.8	00.6	00.0	10.6
	01.1	00.5	00.9	00.0	00.0
	15.0	--	15.0	00.0	00.0
	01.8	00.2	01.7	00.0	15.2
	02.3	00.2	02.0	00.0	00.0
	04.9	00.3	00.9	00.0	00.0
	04.9	02.5	04.8	00.0	10.6
	02.2	00.7	02.1	00.0	00.0
	00.1	00.3	00.0	00.0	00.0
$\overline{X}$	05.4	00.6	04.3	00.0	04.1
S.D.	05.6	00.6	05.3	00.0	06.2
Large prey fish, without morph					
	15.0	--	15.0	00.0	00.0
	15.0	--	15.0	00.0	00.0
	15.0	--	15.0	00.0	18.7
	07.9	00.3	07.8	00.0	13.1
	00.7	00.5	00.2	00.0	00.0
	15.0	--	15.0	00.0	00.0
	01.6	00.4	01.1	00.0	00.0
	04.2	00.3	01.5	00.0	00.0
	04.7	00.5	04.7	00.0	00.0
	02.6	00.0	01.8	00.0	16.1
	03.9	00.8	00.6	00.0	18.7
	05.7	00.3	04.8	00.0	00.0
	05.7	00.3	00.5	00.0	13.1
	14.5	00.8	07.9	22.2	18.7
	01.0	00.6	00.9	49.1	09.3
$\overline{X}$	07.5	00.4	06.1	04.7	07.2
S.D.	05.7	00.2	06.1	13.5	08.3

Table 51: ANOVA analysis of timed behaviour variables from pike experiments. Factorial anova output from SPSS program at University of Alberta, raw data from Tables 49 and 50. Factors = morph, experiment type and size.

Source of Variation	Sum of Squares	df	Mean Square	F	Sig. of F
Total Activity					
Morph	616.728	1	616.728	0.586	0.445
Exp. Type	25,035.293	1	25,035.293	23.776	0.000
Size	33,942.699	2	16,971.348	16.117	0.000
Morph x Exp. Type	7.906	1	7.906	0.008	0.931
Morph x Size	2,240.385	2	1,120.193	1.064	0.348
Exp. Type x Size	5,321.289	2	2,660.645	2.527	0.083
Morph x Exp. Type x Size	3,010.062	2	1,505.031	1.429	0.243
Explained	69,906.188	11	6,355.105	6.035	0.000
Residual	168,476.250	160	1,052.977		
Total	238,382.438	171	1,394.049		
Jerky Swim					
Morph	265.893	1	265.893	0.306	0.581
Exp. Type	44,301.348	1	44,301.348	51.039	0.000
Size	4,139.867	2	2,069.934	2.385	0.095
Morph x Exp. Type	27.435	1	27.435	0.032	0.859
Morph x Size	1,165.491	2	582.746	0.671	0.512
Exp. Type x Size	4,078.047	2	2,039.023	2.349	0.099
Morph x Exp. Type x Size	1,843.958	2	921.979	1.062	0.348
Explained	55,809.188	11	5,073.563	5.845	0.000
Residual	138,879.000	160	867.994		
Total	194,688.188	171	1,138.527		

Source of Variation	Sum of Squares	df	Mean Square	F	Sig. of F
Scull					
Morph	206.851	1	206.851	0.296	0.587
Exp. Type	1,696.545	1	1,696.545	2.429	0.121
Size	6,944.402	2	3,472.201	4.972	0.008
Morph x Exp. Type	54.326	1	54.326	0.078	0.781
Morph x Size	1,165.024	2	582.512	0.834	0.436
Exp. Type x Size	1,949.079	2	974.539	1.395	0.251
Morph x Exp. Type x Size	1,284.841	2	642.420	0.920	0.401
Explained	13,214.438	11	1,201.313	1.720	0.073
Residual	111,739.813	160	698.374		
Total	124,954.250	171	730.727		
Fast Swim					
Morph	4.542	1	4.542	0.022	0.882
Exp. Type	32.876	1	32.876	0.160	0.690
Size	4,655.742	2	2,327.871	11.314	0.000
Morph x Exp. Type	142.392	1	142.392	0.692	0.407
Morph x Size	21.472	2	10.736	0.052	0.949
Exp. Type x Size	87.625	2	43 812	0.213	0.808
Morph x Exp. Type x Size	66.294	2	33.147	0.161	0.851
Explained	5,034.469	11	457.679	2.224	0.016
Residual	32,920.766	160	205.755		
Total	37,955.234	171	221.960		
Frozen					
Morph	739.386	1	739.386	0.724	0.396
Exp. Type	23,523.902	1	23,523.902	23.030	0.000
Size	37,916.801	2	18,958.398	18.560	0.000
Morph x Exp. Type	102.186	1	102.186	0.100	0.752
Morph x Size	1,794.589	2	897.294	0.878	0.417
Exp. Type x Size	7,485.707	2	3,742.854	3.664	0.028
Morph x Exp. Type x Size	2,709.046	2	1,354.523	1.326	0.268
Explained	73,915.750	11	6,719.613	6.579	0.000
Residual	163,430.688	160	1,021.442		
Total	237,346.438	171	1,387.991		

Source of Variation	Sum of Squares	df	Mean Square	F	Sig. of F.
In Cover					
Morph	2,008.103	1	2,008.103	1.991	0.160
Exp. Type	5,624.574	1	5,624.574	5.576	0.019
Size	38,136.875	2	19,068.438	18.905	0.000
Morph x Exp. Type	110.044	1	110.044	0.109	0.742
Morph x Size	9,138.469	2	4,569.234	4.530	0.012
Exp. Type x Size	5,733.547	2	2,866.773	2.842	0.061
Morph x Exp. Type x Size	3,923.146	2	1,961.573	1.945	0.146
Explained	64,077.875	11	5,825.258	5.775	0.000
Residual	161,380.250	160	1,008.626		
Total	225,458.125	171	1,318.469		
In Vegetation					
Morph	75.103	1	75.103	0.158	0.692
Exp. Type	3,657.928	1	3,657.928	7.677	0.006
Size	2,811.876	2	1,405.938	2.951	0.055
Morph x Exp. Type	37.278	1	37.278	0.078	0.780
Morph x Size	871.542	2	435.771	0.915	0.403
Exp. Type x Size	1,658.249	2	829.125	1.740	0.179
Morph x Exp. Type x Size	598.619	2	299.310	0.628	0.535
Explained	9,705.375	11	882.307	1.852	0.050
Residual	76,233.063	160	476.457		
Total	85,938.438	171	502.564		
Dorsals Erect					
Morph	2,287.743	1	2,287.743	2.203	0.140
Exp. Type	17,135.504	1	17,135.504	16.499	0.000
Size	34,280.004	2	17,140.000	16.503	0.000
Morph x Exp. Type	439.483	1	439.483	0.423	0.516
Morph x Size	4,715.715	2	2,357.857	2.270	0.107
Exp. Type x Size	3,549.536	2	1,774.768	1.709	0.184
Morph x Exp. Type x Size	859.155	2	429.577	0.414	0.662
Explained	63,843.438	11	5,803.945	5.588	0.000
Residual	166,176.125	160	1,038.601		
Total	230,019.563	171	1,345.144		

Source of Variation	Sum of Squares	df	Mean Square	F	Sig. of F.
Survival Time					
Morph	0.000	1	0.000	0.000	0.995
Size	293.416	2	146.708	14.001	0.000
Morph x Size	97.765	2	48.883	4.665	0.013
Explained	394.998	5	79.000	7.539	0.000
Residual	586.806	56	10.479		
Total	981.804	61	16.095		
Manipulation Time					
Morph	0.429	1	0.429	2.424	0.125
Size	2.937	2	1.469	8.301	0.001
Morph x Size	0.273	2	0.136	0.771	0.468
Explained	3.665	5	0.733	4.143	0.003
Residual	9.908	56	0.177		
Total	13.574	61	0.223		
Time to First Orientation					
Morph	2.089	1	2.089	0.283	0.597
Size	138.621	2	69.310	9.382	0.000
Morph x Size	3.967	2	1.984	0.269	0.765
Explained	150.009	5	30.002	4.061	0.003
Residual	413.686	56	7.387		
Total	563.694	61	9.241		

Table 52: Factor matrix using principal components, no iterations (initial solution, no simplification).

	Components									
Variable	1	2	3	4	5	6	7	8	9	10
Morph	-0.08549	-0.04823	0.26133	-0.30950	0.89989	0.00766	-0.07245	-0.03197	-0.10076	-0.00043
Size	0.56207	0.20200	0.47213	-0.04664	0.02254	-0.27262	0.38909	0.32732	0.29126	-0.00149
Jerky	-0.59961	0.42861	-0.19165	0.28055	0.17805	0.06659	0.52385	-0.15971	-0.06750	0.02647
Scull	-0.63047	0.26480	0.38912	-0.49687	-0.28606	0.09142	-0.19080	0.07099	0.03271	0.03723
Fast	-0.30279	-0.71466	-0.05055	0.20451	0.08625	0.34521	0.08598	0.46605	0.04033	0.01906
Frozen	0.90875	-0.15651	-0.10760	0.16515	0.08756	-0.23101	-0.15584	-0.15148	-0.00313	0.05045
In cover	0.64053	0.38393	0.16937	0.06041	-0.08806	0.32730	0.02790	0.25645	-0.47808	-0.00049
In vegetation	0.53279	0.21335	-0.15965	-0.17578	0.07553	0.68920	0.01407	-0.15911	0.32865	0.00034
Retreats	-0.26839	0.52625	0.07701	0.59892	0.19041	0.00687	-0.42052	0.20663	0.17479	-0.00029
Jumps	-0.04457	-0.30914	0.73790	0.39802	-0.10066	0.20404	0.03707	-0.38204	-0.02055	-0.00277
Eigenvalue[1]	2.76592	1.39763	1.09808	1.04432	0.99880	0.88351	0.67833	0.65859	0.46979	0.00501
Percent of[2] Variance	27.7	14.0	11.0	10.4	10.0	8.8	6.8	6.6	4.7	0.1

1. Eigenvalue = Σ (loadings for a factor)^2
2. Percent = (eigenvalue ÷ N variables) X 100

Table 53: Factor matrix using principal components, no iterations (initial solution, first simplification = components with eigenvalues less than 0.9 are deleted).

	Component				
Variable	1	2	3	4	5
Morph	-0.08549	-0.04823	0.26133	-0.30950	0.89989
Size	0.56207	0.20200	0.47213	-0.04664	0.02254
Jerky	-0.59961	0.42861	-0.19165	0.28055	0.17805
Scull	-0.63047	0.26480	0.38912	-0.49687	-0.28606
Fast	-0.30279	-0.71466	-0.05055	0.20451	0.08625
Frozen	0.90875	-0.15651	-0.10760	0.16515	0.08756
In cover	0.64053	0.38393	0.16937	0.06041	-0.08806
In vegetation	0.53279	0.21335	-0.15965	-0.17578	0.07553
Retreats	-0.26839	0.52625	0.07701	0.59892	0.19041
Jumps	-0.04457	-0.30914	0.73790	0.39802	-0.10066

Components 1-5 account for 73.1% of the total variance

Table 54: Varimax rotated factor matrix (final solution, first simplification).

	Component				
Variable	1	2	3	4	5
Morph	-0.02148	-0.02693	0.01679	-0.00163	0.99098
Size	0.66619	0.11615	-0.16573	0.28745	0.12210
Jerky	-0.22543	-0.24265	0.73891	-0.18381	0.03009
Scull	-0.00258	-0.97252	-0.00356	0.04190	0.01317
Fast	-0.71999	0.16394	-0.15393	0.28701	0.05395
Frozen	0.41499	0.78533	-0.32603	0.01818	-0.03533
In cover	0.72393	0.24626	-0.02398	0.03733	-0.10526
In vegetation	0.44752	0.27082	-0.16600	-0.29721	0.04443
Retreats	0.10045	0.01655	0.84809	0.14202	-0.00780
Jumps	-0.02263	-0.02743	0.00028	0.89963	-0.00200

The Method of Factor Analysis

Factor analysis is one of a variety of multi-variate analyses which are useful when dealing with large bodies of data. The following description is based entirely upon Huntingford (1973, 1976), Nie et. al. (1975) and Rummel (1970).

Factor analysis fulfills three uses: 1) exploratory - the search for and detection of patterning between variables to discover relationships, new concepts and to reduce the data. 2) confirmatory - testing of hypotheses about variable structuring, 3) measuring - construction of indices to be used as new variables in later analysis. In the present case the factor analysis was used primarily in its first function and to some extent in the second capacity.

Several methods of factor analysis, differing in their approach to the data, are available. The simplest is Principal Components Analysis (PCA). This is a mathematical technique which transforms a given set of variables into a new uncorrelated (orthogonal) set of composite variables or principal components by the model:

$$Z_j = a_{j1}F_1 + a_{j2}F_2 + \dots + a_{jn}F_n$$

where F = components,
1 to n = observed variables,
Z_j = variable j standardized, and
a_j = standardized multiple regression coefficient of variable j on factor i (factor loading).

The coefficients are chosen so that Z_1 represents as large a portion of the original variance as possible; Z_2 the next largest and so on.

Usually the first m components (smaller than the number of variables) account for most of the variance. Matrix algebra and the geometry of multi-dimensional space are algebraic and visual representations of the PCA procedures.

Using my data as an example, the variables (morph, size, jerky, scull, fast, frozen, in cover, in vegetation, retreats and jumps) of expected importance in a predatory situation, may be represented as axes in a space of 10 dimensions. The position of each fish with respect to these axes is a point in this space. The position of all 86 fish is a cloud of points in 10-dimensional space. This cloud is an ellipsoid (a function of the normalization). The major axis (maximum variance) of this ellipsoid is taken as the new first axis of the data (first component). The direction of this axis may be specified by the angles it makes with the 10 original axes of the data. These angles are the loadings of the first component (Table 52).

The PCA next extracts a second component orthogonal to the first which maximizes the remaining original variance along itself. This is repeated until there are as many new axes as there were original variables (Table 52).

The SPSS subprogram FACTOR performs these functions in matrix algebra by first calculating a correlation matrix between all variables then second, extraction of the latent roots of this matrix and the associated latent vectors. The latent roots or eigenvalues (Table 52) are the proportion of the total variance accounted for by each factor. The latent vectors (eigenvectors) are the loadings of each variable on each factor (i.e., $\hat{a}_{jn}$ in the above equation).

The loadings of each variable on the component give the following information:

- each loading is a regression coefficient of the component used to describe a given variable so the relative weight of each variables contribution to the component is given by the loading values.

- the total variance of each independent variable (component) which accounts for the proportion of variance in the dependent variables (morph to jumps) is given by: $(\text{loading})^2$. The proportion of the variance of the variable accounted for by all factors is the sum of all squares of the respective loadings (eigenvalue).

- correlation between variables is given by: $r_{12} = r_1F_1r_2F_1 + \ldots + r_1F_nr_2F_n$ where r_{12} = correlation coefficient between variables 1 and 2; r_1, r_2 = loadings of variables 1 and 2 for the respective component and F_1 = respective component. Thus high correlations (negative or positive) between variables are implied by high loadings (negative or positive) on the same component.

PCA has restated the interrelationships of the original data as new uncorrelated axes (Table 52) but this solution is still complicated. At this point the first simplification may be applied, that is, a minimum eigenvalue is specified and all the variance in the data due to components below this value is ignored (Table 53). The choice of the minimum eigenvalue is arbitrary and it should be remembered that discarding data may result in the loss of valuable information.

The question now arises whether these new axes provide the best fit to the original data. Axis rotation may provide a better fit of the axes to the data and simplify the component structure.

Several methods of rotation of axes are possible. Orthogonal rotation maintains the lack of correlation between the axes and is the most simple. Oblique rotation allows the axes to become correlated,thus may be more biologically meaningful but the interpretation is more difficult. For simplicity sake an orthogonal rotation was chosen. Several methods of orthogonal rotation are possible, each standardized to certain simplifying criteria. Varimax rotation, the commonest method, attempts to maximize the variance of the loadings upon each factor. It was used in the present case (Table 54).

Until now the underlying derivations from the data have been referred to as components (strictly applied to an unrotated solution). Upon rotation the notation 'factors' is used to indicate the derived final solution.

The final solution may now be simplified a second time. This simplification is to delete variables which do not significantly load upon each of the factors. There is no accepted method of assessing the significance of the loadings so in the present case an arbitrary but constant rule was applied. Loadings less than an absolute value of 0.30 (i.e., $0.30^2 = 0.09$ of factor variance accounted for) were deleted.

The final, simplified solution may now be interpreted.

APPENDIX 7

Data Related to Pike Stomach Analyses

Table 55: Frequency of items in stomachs of pike from Wakomao Lake.

1976 Stomachs (N=40):

Diet Item	Number	% of Total
with morph	60	23.3
intermediate (left spine)	0	0.0
intermediate (right spine)	1	0.4
intermediate (spineless)	3	1.1
without morph	8	3.1
unidentified with	38	14.7
unidentified intermediate	1	0.4
unidentified without	14	5.4
unidentified *Culaea*	128	49.6
other species	5	1.9
Total	258	100.0
empty	9	22.5
Total *Culaea* (identifiable)	253/258	98.1

	Dorsal Spine Number		
Morph	4	5	6
with	1 (1.5)	35 (52.2)	11 (16.4)
intermediate	0 (0.0)	5 (07.5)	2 (02.9)
without	0 (0.0)	3 (04.4)	1 (01.5)
unidentified	0 (0.0)	7 (10.4)	2 (02.9)
Total	1 (1.5)	50 (74.6)	16 (23.9)

(% in brackets, N=67 *Culaea*)

1977 Stomachs

Diet Item	Number	% of Total
Small Pike N=95, 18-28 cm Standard Length:		
with morph	28	8.4
intermediate (left)	0	0.0
intermediate (right)	0	0.0
intermediate (spineless)	4	1.2
without morph	6	1.8
unidentified with	15	4.5
unidentified intermediate	2	0.6
unidentified without	6	1.8
unidentified *Culaea*	107	32.1
other fish species (*Pimephales promelas*)	40	12.0
unidentified fish	35	10.5
invertebrates	90	27.0
Subtotal	333	100.0
empty	14	14.7
Large Pike N=26, 40-64 cm Standard Length:		
with morph	12	13.2
intermediate (left)	1	1.1
intermediate (right)	0	0.0
intermediate (spineless)	1	1.1
without morph	1	1.1
unidentified with	15	16.5
unidentified intermediate	0	0.0
unidentified without	5	5.5
unidentified *Culaea*	25	27.5
other fish species (*Esox*)	2	2.2
unidentified fish	27	29.7
invertebrates	2	2.2

Diet Item	Number	% of Total
Subtotal	91	100.0
empty	13	50.0
Total	228/424	53.8

	Dorsal Spine Number		
Morph	4	5	6
with	0 (0.0)	19 (38.0)	8 (16.0)
intermediate	0 (0.0)	2 (04.0)	3 (06.0)
without	0 (0.0)	5 (10.0)	1 (02.0)
unidentified	0 (0.0)	8 (16.0)	4 (08.0)
Total	0 (0.0)	34 (68.0)	16 (32.0)

(% in brackets, N=50 Culaea)

Table 56: Samples from the lake for comparison to stomach samples.

1976 (taken on 18 August):

Morph	Number	% of Total
with	324	67.9
intermediate (left)	14	2.9
intermediate (right)	12	2.5
intermediate (spineless)	16	3.4
without	111	23.3
Total	477	100.0

	Dorsal Spine Number		
Morph	4	5	6
with	8 (1.7)	225 (47.2)	90 (18.9)
intermediate	1 (0.2)	85 (17.8)	25 (05.2)
without	1 (0.2)	34 (07.1)	7 (01.5)
Total	10 (2.1)	344 (72.1)	122 (25.6)

(% in brackets, N=477)

1977 (taken between 20 July and 18 August):

	Number					
	20 July	28 July	11 Aug.	18 Aug.	Total	% of Total
with	251	72	88	110	520	72.6
intermediate (left)	7	0	3	5	15	2.1
intermediate (right)	2	0	3	0	5	0.7
intermediate (spineless)	8	6	3	7	24	3.3
without	72	23	32	26	152	21.2
Total	340	101	129	148	716	100.0

(X^2=4.04, p>>0.05 at 6 df; i.e. no difference in subsample frequencies)

Morph	Dorsal Spine Number 4	5	6
with	7 (2.1)	159 (46.8)	85 (25.0)
intermediate	0 (0.0)	9 (02.6)	8 (02.3)
without	3 (0.9)	49 (14.4)	20 (05.9)
Total	10 (2.9)	217 (63.8)	113 (33.2)

(% in brackets, N=340, 20 July sample)

Table 57: Pelvic morph frequency by size group for each year (confirmed morphs only). Chi-square is goodness of fit.

1976 (collection #76-4):

Pelvic Morph	Lake Sample			Stomach Sample			Electivity Index
	Mean SL(mm)	Frequency	Percent	Mean SL(mm)	Frequency	Percent	
Small (15-29.9 mm)							
with	22.4	264	70.0	22.1	37	84.0	+0.091
intermediate	22.2	27	7.2	25.6	1	2.3	-0.516
without	22.4	86	22.8	23.3	6	13.6	-0.253
Total		377			44		
$X^2 = 4.37$ ($p \cong 0.1$)							
Medium (30-39.9 mm)							
with	34.9	43	64.2	35.5	10	76.9	+0.090
intermediate	35.3	10	14.9	35.1	2	15.4	+0.017
without	34.5	14	20.9	35.3	1	7.7	-0.461
Total		67			13		
$X^2 = 1.42$ ($p \cong 0.5$)							
Large (40+ mm)							
with	45.5	17	51.5	49.4	13	86.7	+0.255
intermediate	48.3	5	15.1	52.6	1	6.7	-0.385
without	44.5	11	33.3	48.9	1	6.7	-0.665
Total		33			15		
$X^2 = 7.51$ ($0.01 < p < 0.025$)							

1977 (collection #77-14-a, 77-16, 77-19-i, 77-20-f):

Pelvic Morph	Lake Sample			Stomach Sample			Electivity Index
	Mean SL(mm)	Frequency	Percent	Mean SL(mm)	Frequency	Percent	
Small (15-29.9 mm)							
with	24.7	323	72.1	27.4	14‡	82.3	+0.066
intermediate	25.3	24	5.3	28.9	1	5.9	+0.053
without	25.1	101	22.5	29.2	2	11.8	-0.312
Total		448			17		
$X^2 = 1.14$ ($p \cong 0.6$)							
Medium (30-39.9 mm)							
with	33.4	184	73.0	36.2	18	78.3	+0.035
intermediate	33.9	19	7.5	32.7	2	8.7	+0.074
without	33.1	49	19.4	38.0	3	13.0	-0.197
Total		252			23		
$X^2 = 0.61$ ($p > 0.9$)							
Large (40+ mm)							
with	43.0	13	81.3	49.6	7	58.3	-0.165
intermediate	41.5	1	6.3	44.2	3	25.0	+0.597
without	41.5	2	12.5	42.5	2	16.7	+0.144
Total		16			12		
$X^2 = 7.69$ ($0.01 < p < 0.025$)							

‡ one with morph was not measureable so is excluded from this table.

Table 58: Pelvic morph frequencies by standard length categories (data for Figures 5 and 6).

1976

		Prey Standard Length Category (mm)										
		15	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	Total
All (lake)	#	0	123	143	111	28	39	21	7	5	0	477
	%	0.0	25.8	30.0	23.3	5.9	8.1	4.4	1.5	1.0	0.0	100.0
All (stomach)	#	0	9	28	14	10	10	7	10	16	6	110
	%	0.0	8.2	25.5	12.7	9.1	9.1	6.3	9.1	14.5	5.5	100.0
With (lake)	#	0	87	101	76	17	26	12	3	2	0	324
	%	0.0	26.9	31.2	23.5	5.2	8.0	3.7	0.9	0.6	0.0	100.0
With (stomach)	#	0	9	24	10	9	5	5	8	11	5	86
	%	0.0	10.5	27.9	11.6	10.5	5.8	5.8	9.3	12.8	5.8	100.0
Intermediate (lake)	#	0	7	12	8	4	6	1	2	2	0	42
	%	0.0	16.7	28.6	19.0	9.5	14.3	2.4	4.8	4.8	0.0	100.0
Intermediate (stomach)	#	0	0	0	1	1	1	0	0	1	0	4
	%	0.0	0.0	0.0	25.0	25.0	25.0	0.0	0.0	25.0	0.0	100.0
Without (lake)	#	0	29	30	27	7	7	8	2	1	0	111
	%	0.0	26.1	27.0	24.3	6.3	6.3	7.2	1.8	0.9	0.0	100.0
Without (stomach)	#	0	0	4	3	0	4	2	2	4	1	20
	%	0.0	0.0	20.0	15.0	0.0	20.0	10.0	10.0	20.0	5.0	100.0

1977

		Prey Standard Length Category (mm)										
		15	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	Total
All (lake)	#	1	34	160	253	182	70	16	0	0	0	716
	%	0.1	4.7	22.3	35.3	25.4	9.8	2.2	0.0	0.0	0.0	100.0
All (stomach)	#	0	0	4	19	20	22	12	5	1	0	83
	%	0.0	0.0	4.8	22.9	24.1	26.5	14.5	6.0	1.2	0.0	100.0
With (lake)	#	0	16	118	189	132	52	13	0	0	0	520
	%	0.0	3.1	22.7	36.3	25.4	10.0	2.5	0.0	0.0	0.0	100.0
With (stomach)	#	0	0	3	17	18	16	5	4	1	0	64
	%	0.0	0.0	4.6	26.6	28.1	25.0	7.8	6.3	1.6	0.0	100.0
Intermediate (lake)	#	0	4	8	12	14	5	1	0	0	0	44
	%	0.0	9.1	18.2	27.3	31.8	11.4	2.3	0.0	0.0	0.0	100.0
Intermediate (stomach)	#	0	0	0	1	1	1	3	1	0	0	7
	%	0.0	0.0	0.0	14.3	14.3	14.3	42.9	14.3	0.0	0.0	100.0
Without (lake)	#	1	14	34	52	36	13	2	0	0	0	152
	%	0.7	9.2	22.4	34.2	23.7	8.5	1.3	0.0	0.0	0.0	100.0
Without (stomach)	#	0	0	1	1	1	5	4	0	0	0	12
	%	0.0	0.0	8.3	8.3	8.3	41.7	33.3	0.0	0.0	0.0	100.0

Combined 1976 and 1977

		Prey Standard Length Category (mm)										
		15	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	Total
All (lake)	#	1	157	303	364	210	109	37	7	5	0	1193
	%	0.0	13.2	25.4	30.5	17.6	9.1	3.1	0.6	0.4	0.0	100.0
All (stomach)	#	0	9	32	33	30	32	19	15	17	6	193
	%	0.0	4.7	16.6	17.1	15.5	16.6	9.8	7.8	8.8	3.1	100.0
With (lake)	#	0	103	219	265	149	78	25	3	2	0	844
	%	0.0	12.2	25.9	31.4	17.7	9.2	3.0	0.3	0.2	0.0	100.0
With (stomach)	#	0	9	27	27	27	21	10	12	12	5	150
	%	0.0	6.0	18.0	18.0	18.0	14.0	6.7	8.0	8.0	3.3	100.0
Intermediate (lake)	#	0	11	20	20	18	11	2	2	2	0	86
	%	0.0	12.8	23.3	23.3	20.9	12.8	2.3	2.3	2.3	0.0	100.0
Intermediate (stomach)	#	0	0	0	2	2	2	3	1	1	0	11
	%	0.0	0.0	0.0	18.2	18.2	18.2	27.3	9.1	9.1	0.0	100.0
Without (lake)	#	1	43	64	79	43	20	10	2	1	0	263
	%	0.4	16.4	24.3	30.0	16.3	7.6	3.8	0.8	0.4	0.0	100.0
Without (stomach)	#	0	0	5	4	1	9	6	2	4	1	32
	%	0.0	0.0	15.6	12.5	3.1	28.1	18.7	6.2	12.5	3.1	100.0

		Prey Standard Length Category (mm)										
		15	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	Total
1976												
Small Pike (N=2)	#	0	1	0	0	0	1	0	1	0	0	3
	%	0.0	33.3	0.0	0.0	0.0	33.3	0.0	33.3	0.0	0.0	100.0
Large Pike (N=38)	#	0	8	28	14	10	9	7	9	16	6	107
	%	0.0	7.5	26.2	13.1	9.3	8.4	6.5	8.4	15.0	5.6	100.0
1977												
Small Pike (N=95)	#	0	0	4	11	9	12	9	5	1	0	51
	%	0.0	0.0	7.8	21.6	17.6	23.5	17.6	9.8	1.9	0.0	100.0
Large Pike (N=26)	#	0	0	0	8	11	10	3	0	0	0	32
	%	0.0	0.0	0.0	25.0	34.4	31.2	9.7	0.0	0.0	0.0	100.0
Combined												
Small Pike (N=97)	#	0	1	4	11	9	13	9	6	1	0	54
	%	0.0	1.9	7.4	20.4	16.7	24.1	16.7	11.1	1.9	0.0	100.0
Large Pike (N=64)	#	0	8	28	22	21	19	10	9	16	6	139
	%	0.0	5.7	20.1	15.8	15.1	13.7	7.2	6.5	11.5	4.3	100.0